VOLUME XXX NUMBER 3

BOTANICAL GAZETTE

SEPTEMBER, 1900

ORIGIN OF THE CONES OF THE MULTIPOLAR SPINDLE IN GLADIOLUS.

ANSTRUTHER A. LAWSON.

(WITH PLATE XII)

RECENT investigation in cytology has gone far to establish the fact that multipolar spindles are of very general occurrence in the higher plants. It is indeed held by many investigators that the origin and development of the karyokinetic spindle in these plants is diametrically opposed to that which prevails in the lower plants and animals. These observers believe that the spindle, instead of being bipolar from the first and under the control of a kinetic center, passes through a series of multipolar stages in the course of its development. The problem has thus become exceedingly interesting and important, and calls for vigorous and careful investigation.

Multipolar spindles have been found in Lilium by Farmer (1893), in Larix by Belajeff (1894) and Strasburger (1896), in Equisetum by Osterhout (1897), in Lilium, Fritillaria, Helleborus, Podophyllum, and Pinus by Mottier (1897, *a* and *b*), in Hemerocallis by Juel (1897), in Chara by Debski (1897), in Zamia by Webber (1898), in Sagittaria by Schaffner (1898), in Nymphaea and Nuphar by Guignard (1898), in Hesperaloe, Hedera, Disporum, Smilacina, Gladiolus, Iris, and Cobaea by Lawson (1898), in Passiflora by Williams (1899), in Solanum by Nemec (1899), and in Convallaria and Potamogeton by Wiegand (1899).

Occurring in such a wide range of forms, and having been demonstrated by various methods of fixing and staining, it seems extremely improbable that the phenomenon is abnormal or due to artifact. Such a conclusion is much strengthened by the fact that in none of the higher plants has the animal type of spindle formation been discovered. While it is true that some investigators (Guignard, Schaffner, Fullmer, etc.) have described and figured granules situated at the poles of the spindle, and thus in some respects resembling centrosomes, in no case have such granules been observed to take an actual part in the formation of the achromatic figure as it occurs in animals.

Assuming then that the multipolar type is the normal type of spindle formation in the higher plants, since Strasburger and other authorities cannot reconcile the function of a kinetic center with such a process, we are confronted with two problems, namely, the manner in which the multipolar spindle becomes bipolar, and the origin of the cones.

No explanation has yet been offered that will reasonably account for the ultimate bipolarity of the spindle beyond the mere statement that certain of the cones fuse and arrange themselves in two groups. Such an explanation was first suggested by Belajeff (1894), and was later confirmed by Osterhout (1897), Mottier (1897), and others. How this fusion is brought about is still uncertain. Even Guignard (1898), who describes centrosomes situated at the apices of the cones in Nymphaea and Nuphar, states that he is "unable to suggest, at present, in what manner the multipolar spindle becomes bipolar." So that with or without centrosomes the phenomenon is unaccounted for, and we must therefore wait for the light of future investigation.

On the origin and development of the cones much more encouraging results have been obtained. The investigations of Belajeff (1894) and Strasburger (1896) on Larix, Osterhout (1897) on Equisetum, Mottier (1897) on Lilium, Juel (1897) on Hemerocallis, and more recently those of Nemec on Solanum and Allium, and Davis on Anthoceros, have thrown considerable

light on the subject. But while these observers all agree that the spindle arises from a weft of kinoplasmic threads, very few observations have been made on the very earliest stages of the development of the cones; probably on account of the fact that these early stages are very difficult to obtain. In 1898, however, the writer was fortunate enough to obtain a very complete series of these early stages in the pollen-mother cells of *Cobaea scandens*. In this case it was found that, as division approaches, the nucleus becomes surrounded by a zone of granular substance which differs in structure and staining properties from the rest of the cytoplasm. This zone is so constant that it was proposed to designate it perikaryoplasm, and as it has been found in several other genera, the writer feels justified in using the term in the present paper. Upon the breaking down of the nuclear wall, the perikaryoplasm forms a central network of kinoplasmic fibers which grows out into several projections. By their growth outward these projections become the cones of the multipolar figure. The spindle fibers are therefore formed by the elongation of the meshes of the net-work in the direction of the projections.

Encouraged by these results the writer was led to pursue his investigation of these early stages in other forms. His observations on Gladiolus proved so interesting that it was thought advisable to record them, believing that they will throw further light on this much disputed problem.

The method employed in preparing the material was practically the same as that adopted in my work on Cobaea, namely: Flemming's strong solution of chromic-osmic-acetic acid, diluted with one volume of water, was used for fixing, and the triple stain, safranin, gentian-violet and orange G, for staining. I would here like to emphasize the importance of fixing the material in the field, because of all the material I have examined it was only in those anthers which were fixed *immediately* after being detached from the plant that the early multipolar stages were found. After being fixed the anthers were thoroughly washed in running water from six to eight hours, and were then

dehydrated by being passed through various grades of alcohol. Bergamot oil was used to precede the infiltration of paraffin. Microtome sections from 3.6 μ to 6 μ thick were used.

THE POLLEN MOTHER CELLS OF GLADIOLUS.[1]

Gladiolus affords very exceptional material for the study of spindle formation on account of the large size of its anthers, pollen mother cells, and nuclei. The cytoplasm in the resting pollen mother cell appears in the form of a clear uniform reticulum, with numerous small spherical bodies scattered irregularly through it. The nucleus is very large, containing a vacuolated nucleolus, and the chromatin in a very characteristic spirem. As division approaches, the cytoplasm undergoes a remarkable differentiation in identically the same manner that occurs at this stage in the corresponding mother cells of Cobaea. While the chromosomes are being formed, there gradually accumulates a complete and sharply differentiated zone of granular substance about the nucleus. In nearly every respect this zone resembles the perikaryoplasm so characteristic of Cobaea. It accumulates in the same manner, has the same structure, and stains in the same fashion. In fact, the only difference that could be detected was in the size of the granules of which the zone is composed. In Gladiolus these granules are very fine, while those in Cobaea are comparatively coarse. We shall therefore continue to use the term perikaryoplasm in the following description.

By the time the chromatin thread breaks up and assumes the form of curved rod-shaped chromosomes, the perikaryoplasm has reached its maximum development. In many cases it was observed that the small black spherical bodies which were scattered irregularly through the cytoplasm had arranged themselves in the form of a ring at the outer margin of the perikaryoplasm. But this peculiarity is not as constant or as striking as it is in Cobaea.

At this early stage in Cobaea it was observed that the nuclear membrane breaks down, but in Gladiolus this does not happen

[1] One of the common cultivated garden forms, probably of the hybrid *G. Gandavensis* (Hort.).

until a much later stage, as can be seen readily in *figs. 1–8*. This fact is significant, because it is quite clear that the method of spindle development depends much upon *when* the nuclear membrane breaks down. This is very well illustrated by the two types which we have before us. In Cobaea, where the nuclear wall breaks down at a very early stage, we have a central network formed which occupies the space of the nuclear cavity. In Gladiolus, where the nuclear wall persists, the network is not formed in this central position, but is formed outside of and immediately surrounding the membrane. This difference also has its effect on the character of the network. When the nuclear wall breaks down at an early stage the nuclear cavity affords a large space for the formation of the network. Its meshes are consequently quite large. On the other hand, when the nuclear wall persists, as it does in Gladiolus, the network appears in the form of a close weft or felted zone.

Very careful observations were made at this stage to see if any of the kinoplasmic threads penetrate the nuclear membrane, as recently observed by Wiegand in Potamogeton. Although hundreds of cells were examined no such penetration was detected.

When this weft or felted zone commences to form, one might at first think that it arose by the fraying out of the nuclear membrane. But as it grows to such a width (*fig. 1*), and the nuclear membrane apparently loses none of its distinctness (*figs. 1–8*), it seems much more probable that it grows at the expense of perikaryoplasm as the central network does in Cobaea.

From the time of its first appearance the felted zone stains very readily with gentian-violet, and as it increases in size its meshes become larger and the sharp kinoplasmic threads of which it is composed are readily distinguished. As soon as the weft reaches a certain size (*fig. 1*), it ceases to grow uniformly, but pushes out into several projections as shown in *fig. 2*. As far as the writer could make out, there appears to be no definite number of these projections. *Fig. 2* shows at least five. Six was the largest number observed in cross-section. Just how

many there are it is impossible to say at present. These projections rapidly increase, and on account of their growth outward the meshes become decidedly elongated. By the time they have reached their full growth, the whole outer portions of the cones are composed of long distinct fibers converging to the apices, and it is only at the base that the meshes of the original weft can be distinguished. The apices of the cones taper out into remarkably sharp points, but in no case was there a body observed at these points which might be considered as a controlling center.

During the entire process of the formation of the cones the nuclear membrane remains intact. It is only after they have reached their full development that it begins to break down. The breaking down of the membrane is shown in *figs.* 6 and 7. It will be seen from these figures that this takes place on one side first, where the identity of the membrane becomes lost in the network at the base of the cones. It will also be observed from these figures that the nucleolus still persists. It remains quite conspicuous until all traces of the nuclear wall are lost, when it suddenly disappears. What eventually becomes of it was not observed.

In my observations on Cobaea it was thought probable that the linin of the nucleus took part in the formation of the central network from which the cones develop. Now in Gladiolus, where the kinoplasmic network and the cones are fully developed before the nuclear wall disappears, it becomes quite evident that the linin takes no essential part in the formation of the achromatic figure.

Upon the disappearance of the nuclear membrane the bases of the cones soon adjust themselves to the space offered by the nuclear cavity, and in doing so come in direct contact, for the first time, with the chromosomes. These latter bodies are not lacking in interest; but as the writer, in future work, hopes to make a more detailed study of the chromatin in Gladiolus and other forms, his observations will not be recorded at present. Soon after this stage a series was observed showing that the

cones first approach each other and finally unite in two groups in the form of a bipolar spindle, as shown in *fig. 10*.

From the above observations, and from previous work on other forms, it would seem that there are several types of spindle development in the higher plants. It would be imprudent to classify all of these probable types until the early stages of many of the forms have been more thoroughly investigated. At present we have at least three forms which have been thoroughly worked out and which differ from one another sufficiently to warrant us in distinguishing them as types. These are represented by Equisetum, Cobaea, and Gladiolus.

SUMMARY.

The above observations may be summarized as follows:

As nuclear division approaches, a granular zone accumulates about the nucleus. This zone in every respect resembles the perikaryoplasm so characteristic of the pollen mother cells of Cobaea.

A close network or felted zone of kinoplasmic fibers is formed immediately outside of and completely surrounding the nuclear wall. This is probably developed from the perikaryoplasm.

This network grows out into several projections which become the cones of the multipolar figure.

The nuclear membrane persists until the cones are almost fully developed.

The spindle fibers are formed by the elongation of the meshes of the network composing the cones.

Neither the nuclear wall, nucleolus, nor linin take any essential part in the formation of the achromatic figure.

The cones of the multipolar figure fuse and arrange themselves in two groups and form a bipolar spindle.

THE UNIVERSITY OF CALIFORNIA.

LITERATURE.

1894. BELAJEFF, W. Zur Kenntniss der Karyokinese bei den Pflañzen. Flora **79**: 430.

1899. DAVIS, B. M. The spore mother cell of Anthoceros. BOT. GAZ. **28**: 89.

1897. DEBSKI, B. Beobachtungen über Kerntheilung bei *Chara fragilis*. Jahrb. f. wiss. Bot. **30**: 227.

1893. FARMER, J. B. On nuclear division in the pollen-mother cells of *Lilium Martagon*. Ann. of Bot. **7**: 392.

1895. ——— Ueber Kerntheilung in Lilium-Antheren besonders in Bezug auf die Centrosomenfrage. Flora **80**: 56.

1898. FULLMER, E. L. Cell division in pine seedlings. BOT. GAZ. **26**: 239.

1899. ——— The development of the microsporangia and microspores of *Hemerocallis fulva*. BOT. GAZ. **28**: 81.

1898. GUIGNARD, L. Centrosomes in plants. BOT. GAZ. **25**: 158.

1898. ——— Les centres cinétiques chez les végétaux. Ann. des Sci. Nat. Bot. VIII **5**: 178.

1897. JUEL, H. O. Die Kerntheilungen in den Pollenmutterzellen von *Hemerocallis fulva*, und die bei denselben auftretenden Unregelmässigkeiten. Jahrb. f. wiss. Bot. **30**: 205.

1898. LAWSON, A. A. Some observations on the development of the karyokinetic spindle in the pollen-mother cells of *Cobaea scandens*. Proc. Cal. Acad. Sci. III. **1**: 169.

1897*a*. MOTTIER, D. M. Ueber das Verhalten der Kerne bei der Entwickelung des Embryosacks und die Vorgänge bei der Befruchtung. Jahrb. f. wiss. Bot. **31**: 125.

1897*b*. ——— Beiträge zur Kenntniss der Kerntheilung in den Pollenmutterzellen einiger Dicotylen und Monocotylen. Jahrb. f. wiss. Bot. **30**: 169.

1899*a*. NEMEC, B. Ueber Kern- und Zelltheilung bei *Solanum tuberosum*. Flora **86**: 214.

1899*b*. ——— Ueber die karyokinetische Kerntheilung in der Wurzelspitze von *Allium Cepa*. Jahrb. f. wiss. Bot. **33**: 313.

1897. OSTERHOUT, W. J. V. Ueber Entstehung der karyokinetischen Spindel bei Equisetum. Jahrb. f. wiss. Bot. **30**: 159.

1898. SCHAFFNER, J. H. Karyokinesis in the root tips of *Allium Cepa*. BOT. GAZ. **26**: 225.

1896. STRASBURGER, E. Karyokinetische Probleme. Jahrb. f. wiss. Bot. **33**: 151.

1897. ——— Ueber Cytoplasmastructuren, Kern- und Zelltheilung. Jahrb. f. wiss. Bot. **30**: 375.

1897. WEBBER, H. J. Peculiar structure occurring in the pollen-tube of Zamia. BOT. GAZ. **23**: 453.

1899. WEIGAND, K. M. The development of the microsporangium and microspores in Convallaria and Potamageton. BOT. GAZ. **28**: 328.

1899. WILLIAMS, C. L. The origin of the karyokinetic spindle in *Passiflora cærulea*. Proc. Cal. Acad. Sci. III. **1**: 189.

1
2
4
7

3

6

5

9

10

EXPLANATION OF PLATE XII.

Figures drawn with Abbe's camera lucida, Zeiss homog. immersion objective one twelfth, apert. 1.25, compensating ocular no. 6.

FIG. 1. A pollen mother cell showing the cytoplasm differentiated into three zones; the outer cytoplasm stains a light gray-blue; the perikaryoplasm stains a light orange, and the weft or felted zone of kinoplasmic fibers stains blue; the nuclear wall is intact and the nucleus contains a large nucleolus and several curved chromosomes, with a small amount of linin threads.

FIG. 2. The weft of kinoplasmic threads is commencing to push out into several projections, preparatory to forming the cones of the multipolar figure; the network of the weft appears more distinctly.

FIG. 3. A still later stage in the development of the projection, with distinct cones formed.

FIG. 4. A still later stage showing the elongation of the meshes and the formation of fibers by the pulling out of the network.

FIG. 5. A slightly older stage than that of *fig. 4*.

FIG. 6. A later stage when the cones are nearly fully developed; the outer portions of the cones consist now of distinct fibers, and it is only at the base of the cones that the network of the original weft can be distinguished; the nuclear wall has as yet shown no sign of breaking down, and the nucleolus still persists.

FIG. 7. The first indication of the nuclear wall breaking down. The chromosomes now come in contact with the base of the cones.

FIG. 8. Shows the same as *fig. 7*, but a little more advanced.

FIG. 9. The nuclear wall and the nucleolus have disappeared; several of the cones have fused, and the chromosomes are attached to the fibers at the base of the cones.

FIG. 10. The mature spindle, with the chromosomes at the equator and about to move to the poles.

THE DEVELOPMENT AND FUNCTION OF THE CELL PLATE IN HIGHER PLANTS.

H. G. TIMBERLAKE.

(WITH PLATES VIII AND IX)

(*Concluded from p. 99*)

2. *The genetic stage.*

THE origin of the cell plate elements occurs in the equator of the central spindle. In the onion this brings them in the midst of the carbohydrate zone (*figs. 18, 19*). There seems to be no doubt that they are thickenings of the spindle fibers. In the onion, while they are often very difficult to distinguish at first, owing to the fineness of the fibers and the abundance of carbohydrate material, it can be determined clearly that they are swellings of the fibers (*fig. 29*). There is nothing to suggest the movement of cytoplasmic granules toward the equatorial plane to form the cell plate in the manner described by Treub. Working on living cells, Treub might easily have failed to see the beginning of the cell plate. His statement that it first appears as a fine line would indicate this. The same explanation would apply to the observations of Zacharias, although it is to be noted that Zacharias described special bodies as cell plate elements and not mere undifferentiated cytoplasmic granules such as those of Treub. It is to be doubted, however, whether these bodies have any connection with a cell plate. I do not think it unreasonable to suppose that what Zacharias saw was a substance destined for the formation of the cell wall instead of a cell plate. He may possibly have seen the hyaline spaces between the spindle fibers which I have found stained orange, as above described.[36] The origin of the cell plate elements is shown more clearly in the larch. Here the thickenings are much more pronounced, being elongated bodies instead of small

[36] *Cf.* FARMER, p. 78 of this paper.

nodules (*figs. 4, 27c*). In this case it looks as if the activity of a fiber previously described as beginning near either daughter nucleus and going toward the equator, has become localized at the latter point, producing a swelling on the fiber. The production of such a swelling is accompanied by the further shortening of the fiber (*fig. 27c*), showing that there has been an actual transformation of the substance of the fiber in the formation of the cell plate element. While the above described process seems to agree with the older observations of Strasburger that the substance of the cell plate elements has flowed in the fibers to the equator,[37] it should be noted that there is nothing in the process I have described to indicate a collection of smaller granules within the fiber, but that the fiber itself has changed. The whole process seems to indicate a somewhat plastic character of the fiber.

The time relative to other phases of mitosis at which the cell plate elements occur seems to vary in the onion and the larch. In the former their appearance is concurrent with or closely following that of the carbohydrate material. The chromosomes have begun at this time to form slightly denser masses, preparatory to the reconstruction of the daughter nuclei, but separate chromosomes may still be distinguished. In the larch, the process of reconstruction goes so far before the cell plate elements appear that the daughter nuclei are often clearly outlined (*figs. 3, 4*). Whether this difference has any special significance, I cannot say. It would be interesting to compare a wider variety of forms in this respect.

As soon as the elements can be detected, they seem to form a layer throughout the thickness of the original spindle, indicating that they are simultaneous in their origin. Very early stages may have escaped observation, however, although a careful search was made for them. That such a progressive formation might be the case would be suggested by such figures as *5* and *6*, where there are some peripheral fibers on which cell plate elements have not yet formed. On the other hand, it

[37] *Cf.* p. 75 of this paper.

is probable that all the fibers showing cell plate elements in *fig. 4* are the original connecting fibers, while the peripheral fibers are the previously described radiating fibers. I have previously shown that the changes in the connecting fibers, before the formation of the cell plate elements take place in all of the fibers at the same time, while the radiating fibers have apparently so changed as to form peripheral connecting fibers. Whether all of the connecting fibers form cell plate elements was a point that I could not settle with certainty. It is possible that those connecting fibers which did not show the changes described in the preliminary stages do not form cell plate elements. The phenomena observed in later stages render such a possibility more probable.

After they first become visible, the cell plate elements continue to enlarge in their equatorial diameter until they come into contact with one another and fuse into a continuous plate. This process is accompanied by the further shortening of the fibers. In connection with the shortening of the spindle fibers there is a continued appearance of trophoplasm in the terminal parts of the spindle (*figs. 4, 5*).

The result of the processes just described may be briefly summed up as follows. There is in the spindle a young cell plate formed simultaneously from the substance of the spindle fibers. In the onion it lies in the midst of a zone of reserve carbohydrate material to be used in the formation of the new cellulose wall. In the larch such a zone is not seen at this stage. The cell plate may now be said to begin the next stage in its development.

3. *The growing stage.*

This stage is marked by the following phenomena: The central fibers continue to shorten, adding their substance to the cell plate until they have finally disappeared. The peripheral fibers begin to appear more and more bent and to form cell plate elements. As the central fibers disappear their place is partly taken by granular trophoplasm and the daughter nuclei come to lie nearer the young cell plate. While the peripheral

growth is continuing, the older portion of the cell plate splits and the new wall is laid down between the halves. These processes continue until division is complete. During the period of growth the cell plate may so shift its position as to lie in a plane different from that in which it was first formed.

I have thought it best to describe the above processes separately. The fate of the spindle fibers is a question of much interest here. From the phenomena that I have been able to observe in the cells studied, I have become convinced that all of the fibers that form cell plate elements are completely used up in the growth of the cell plate. A comparison of *figs. 4, 5, 6,* and *7* is instructive on this point. In *fig. 4* the cell plate elements have just formed, the connecting fibers have drawn away from the daughter nuclei, and granular trophoplasm has appeared among the ends of the fibers of the central spindle. In *fig. 5* the cell plate elements have fused into a cell plate, the fibers have shortened still further, and the trophoplasm appears as before. *Fig. 6* is especially important. Here the fibers have become very short and the ends furthest away from the cell plates are no longer surrounded by the granular trophoplasm. These ends appear to be sharp pointed, while the portion of each fiber that is in connection with the cell plate is relatively thick. At a later stage the trophoplasm becomes distributed more throughout the region originally occupied by the central spindle. Here it frequently appears in irregular rows of granules (*fig. 7*). In this latter figure very small portions of the spindle fibers may be seen. They show the typical pointed structure above described and are distinct from the rows of trophoplasm. Throughout all of the processes involved in the formation of the cell plate the spindle fibers and the cell plate itself stain strongly with the violet of the triple stain. I have not observed the gradual transition from the violet to the orange color described by Strasburger[38] for the spindle fibers at the time when the cell plate is formed. Not only do the spindle fibers and the cell plate stain violet, but the plasma membrane of the

[38] Zellhäute.

mother cell frequently shows the same color. To be sure some preparations show the orange color in connection with the cell plate, but the violet of the cell plate itself could nearly always be distinguished. The orange color is probably due to the small amount of carbohydrate material that sometimes appears at this stage. I do not think that the presence of the above mentioned irregular rows of granular trophoplasm is to be taken as evidence that the spindle fibers break up into granular cytoplasm. My preparations show clearly that the spindle fibers are entirely distinct from these rows. The history of the fibers seems to consist of a gradual shortening and thickening until their whole substance is transformed into a cell plate, *i. e.*, a membrane. While the above description will apply to those fibers which take part in the formation of the cell plate, the fate of those radiating fibers which have no part in this process remains unaccounted for. My observations upon this latter point have been too limited to base any conclusions upon them. In a very early stage in the formation of the cell plate these fibers often seem to lose their characteristic radial arrangement and to become more of a tangled mass in the cytoplasm (*figs. 3, 4*). It is possible that they become separated from the daughter nuclei and are finally absorbed into the rest of the protoplasm. There is one other interesting case to be noted. In some cells of the larch and some of the cells of the root tip of Fritillaria, after the cell plate was formed, a few clearly defined fibers were observed in the region between each daughter nucleus and the cell plate. These fibers are probably the same that have been mentioned previously as not showing the stages preparatory to the formation of the cell plate. Their fate was not determined. *Fig. 10* is interesting in this connection. It represents a late stage in the division of the pollen mother cell when the permanent cell plates are complete, but when there still exist numerous fibers all around each nucleus, extending into the cytoplasm and reaching in many cases to the plasma membrane. Whether these are a part of the connecting and radiating fibers that existed during the earlier stages, or new

fibers that have been formed after the division was complete, I did not determine. If the former supposition is true there would seem to be an unusually large number of spindle fibers which took no part in the formation of the cell plate. From the fact that in all cases observed of the formation of the first cell plate no such abundance of regularly arranged fibers was evident, I think it probable that these are mostly new fibers. Connecting stages, however, may have been overlooked. Their significance in either case is not clear. It may be that they build a new plasma membrane around each pollen grain inside of the plasma membrane of the special mother cell. Further investigation upon these late stages of the formation of the pollen grains is desirable.

The process by which the cell plate grows in area is difficult to determine with certainty. By comparing stages represented in *figs. 4–7*, I have concluded that a part of the growth of the cell plate takes place by means of the continued addition to it of the substance of the original fibers until they are entirely used up. I have already described what seems to be the process through which the fibers go in the formation of the cell plate. I consider the evidence for the complete transformation of at least part of the fibers into the cell plate conclusive. The most reasonable interpretation of *fig. 6* seems to me to be that all of the very short fibers here shown are the remains of the connecting spindle fibers shown in *fig. 4*. This interpretation is further strengthened by an examination of an intermediate stage (*fig. 5*). Here the fibers are not much shorter relatively than they are in *fig. 4*, but it is noteworthy that they are further apart, while the cell plate is, of course, more conspicuous. These facts point to the conclusion that the substance of the fibers, collecting in the middle, has simply pushed the fibers further apart, a process that constitutes the growth of the cell plate. While such a simple mechanical process may account for a portion of the growth of the cell plate, there are phenomena which seem to indicate that other processes accompany it. In all of the above figures, while there is a large area throughout in

which the cell plate is in the same stage of development, it will be noted that the peripheral portions show earlier stages, and that there are fibers connected with this latter portion whose substance has not yet been used in the formation of the cell plate. In many cells these fibers show all gradations from very short ones toward the center of the cell to those reaching nearly, if not quite, to the daughter nuclei (*fig. 30*). Some of the latter, instead of extending from one nucleus to the other, extend simply from the nucleus into the cytoplasm of the opposite daughter cell. These facts would indicate that these peripheral fibers are radiating fibers which are taking part in the formation of the cell plate. The fact that the peripheral fibers appear to be more numerous and in a more compact layer in the stages represented by *figs. 6* and *7* than in earlier stages (*fig. 5*) may be explained by the crowding produced by the growth of the cell plate by the transformation of the inner fibers in the fashion described above, *i. e.*, the peripheral fibers in *fig. 6* would represent all of the radiating fibers between the boundary of the cell plate in this figure and its boundary when it had reached a stage such as that shown in *fig. 5*. The appearance of shorter fibers on the inside of the peripheral bundles and longer ones on the outside shows that the process of cell plate formation goes on gradually in these fibers from the inside outward. This is shown farther by the fact that the cell plate elements of the inner fibers have already fused into a cell plate, while the intermediate ones are often distinct, and the outer fibers often show no cell plate elements (*fig. 30*). The foregoing observations seem to show that the increase in area of the cell plate is due to a two-fold process consisting (1) of a continuous transformation of the substance of the original connecting fibers, resulting in the expansion of the portion of the plate around each fiber and the consequent wider separation of the fibers; (2) concurrent with the above method occurs the addition of new cell plate elements to the peripheral portions of the cell plate, and their growth in the same fashion as those previously formed. These latter processes go on in the radiating fibers which have come into

such a relation to the central spindle as to continue the first process of growth.

Another question of importance in this connection is, does the growth in area of the cell plate depend entirely upon the fibers already existing, or are new peripheral fibers formed? So far as my observations upon the larch go, I think it probable that there is no formation of new fibers, but that the whole growth takes place as a result of the changes in the existing fibers; yet the evidence on this point was not conclusive. If the hypothesis is true, whether the mother cell divides into the four cells which form the pollen grains by successive or by simultaneous division depends upon the number of spindle fibers existing in connection with the first nuclear division. If there are enough fibers to form a cell plate completely across the cell, successive division results, while if the cell plate does not reach across the cell it is absorbed into the rest of the protoplasm, and the final division takes place simultaneously after the second nuclear division. In the onion the conditions are such as to indicate the necessity for the formation of new peripheral fibers. It will be remembered that at the time of the formation of the young cell plate there were but few radiating fibers visible, and those that could be seen were relatively short, with the exception of a few near the periphery of the central spindle. In the later stages, after the fibers had entirely disappeared from the central area, the same relations of spindle fibers in the peripheral portion of the spindle could be distinguished that have been previously described in the larch (*fig. 30*). This relation indicates that there has occurred a growth at least of the original radiating fibers, with the probable production of new ones.

There is another point of importance here. The fact that some of the longer peripheral fibers may be traced to the nucleus indicates a continuous production of new peripheral fibers from the nucleus as a center. The difference, then, between the larch and the onion is possibly as follows: in the former the extent of growth of the cell plate depends upon the number of existing fibers, while in the latter, where there is necessity for the

formation of a complete cell plate, the original fibers may be supplemented by the growth of new peripheral fibers. The cases in the larch in which the cell plate is not completed after the first nuclear division are possibly accounted for by the fact that the nucleus has begun to prepare for its second division, and consequently new fibers necessary for the completion of the cell plate are not produced.

Concurrent with the growth of the cell plate in extent and the disappearance of the fibers from a central portion of the spindle the nuclei come to lie nearer the cell plate (*figs. 6, 11*). This phenomenon has often been observed, but no adequate explanation for it has been suggested. From the appearance of the whole cell in the larch it would seem that such a migration of the nuclei is due to the mechanical pressure of the surrounding cytoplasm. While some granular cytoplasm has entered the region occupied by the spindle during the early stages, the later stages show very little addition until the cell plate is nearly complete and all of the spindle fibers have been nearly used up. The fibers seem to form a barrier against its ingress, so that it forms a denser layer around the whole spindle (*fig. 7*). It is possible, too, that the growth of the cell plate by the method previously described has displaced the cytoplasm around the spindle, and that such a displacement results in a greater pressure upon the nuclei.

The history of the carbohydrate material during the growth of the cell plate could not be followed with certainty. I find that it always appears plainly in connection with the spindle fibers which are forming the cell plate. In the older portions of the cell plate, however, where the spindle fibers had entirely disappeared, this substance was often indistinguishable, but in those cases where the cell plate was split, a young cell wall could nearly always be detected. It did not extend, so far as could be seen, the entire length of the cleft, but was only in the older portions (*fig. 31*). A peculiar case was sometimes found in the larch, where an incomplete cell plate appeared with a conspicuous cell wall formed between the halves of the older portion

lying in the cytoplasm, with some of the original fibers still attached to it while the daughter nuclei were again dividing. Whether this cell plate and wall were finally completed, I did not determine. The same stage of development of the cell plate was often observed, in which no cell wall could be detected. The significance of the presence of a cell wall without the previous appearance of the carbohydrate material has already been discussed.

The evidence for the splitting of the cell plate before the formation of the new cell wall need not be discussed in detail here. Treub, in his experiments upon living cells, showed that the splitting occurs, and the new wall is laid down between the separated halves before the cell plate has attained its full growth. My own observations confirm this fact (*figs. 19, 31*). But one point of difference should be noted between Treub's observations and mine. In Treub's figures the beginning of the process is represented on one side of the cell where the cell plate has reached the membrane of the mother cell, while in my preparations it may be clearly seen that the splitting begins in the central region of the plate and extends toward the periphery. The mechanics of such splitting is hard to explain. The fact that no evidence of it was found except where the spindle fibers had disappeared would indicate that the fibers have no part in the process. From his observations on Fucus, where the granules which form the cell plate divide before fusion, Strasburger suggested that the splitting may be the result of a similar process in the higher plants, *i. e.*, the separate cell plate elements may divide before they fuse. If such a division takes place the two parts remain so close together that no evidence of it appears until a much later stage. Where the cell plate elements are so conspicuous as they are in the larch, it is reasonable to expect to find stages showing their division if it really occurs. The lack of such stages seems to me to indicate that the division comes later, after the elements have fused into a continuous plate. If this be true, the problem is that of the splitting of a continuous protoplasmic membrane. Strasburger decided that

there is no change of a middle layer in the cell plate into a cell wall. This conclusion rests mainly upon the fact that the halves of the cell plate which appear after splitting are together equal in thickness to the original plate, *i. e.*, there has been no diminution of the substance of the cell plate during the process of splitting. That the cell wall is not a differentiated portion of the cell plate seems to me to be further shown by those cases in which portions of the separate halves of the cell plate appear with no cell wall between them (*figs. 30, 31*).

The splitting seems to be due primarily to a differentiation of the substance of the plate itself into two layers. Of what this differentiation consists is by no means apparent. It is hard to conceive of a layer of protoplasm becoming differentiated into two separate layers similar in all apparent respects to each other. To be sure, the two layers form the boundaries of separate cells, a fact which may be taken to indicate a possible chemical difference between them. This differentiation, in itself, moreover, would not account for the separation of the halves of the plate. A possible explanation for this latter phenomenon may be that there is secreted between the halves some non-stainable substance, perhaps cell sap, which serves to separate them. The apparent disappearance of the carbohydrate material before the cell plate halves appear separated may mean that there is a change in this substance, preparatory to its being deposited as a wall, of such a character that it does not take the same stain as before. It may be that it simply forms a less dense solution, and that in this form it is first deposited between the halves of the cell plate. The appearance of a stained wall would then mean that the substance had again become dense enough to take the stain. While the above explanations are purely hypothetical, I cannot see that they in any manner do violence to the observed facts. They are suggested only in order to help bring out some phases of the problem to be solved. It should be noted in this connection that the splitting of the cell plate is apparently not quite analogous to the longitudinal splitting of the chromatin thread, unless Strasburger's view that the granules divide before

they fuse into a cell plate is to be accepted. In the splitting of the chromatin thread we may easily imagine the process taking place by constriction, but in the case of a continuous layer of protoplasm like the cell plate such a process would be impossible. The more so when we remember, as my figures show, that the splitting begins in the central portion and extends outward.

The change in position of the cell plate during its growth is shown by *figs. 12* and *21*. The explanation of such a change is not obvious. The figures show that the nuclei do not move with the cell plate. Whether the cell plate ever changes from a true diagonal to a transverse plane I was unable to determine. The figures show only those cases where the plane in which the cell plate was first formed was not a true diagonal. Nemec[39] has shown that the position and form of the young spindle can be determined to some extent by means of pressure or tension exerted upon the tissues in which the dividing cells occur. It is possible in these cases that the conditions of pressure or tension upon the single cells have so changed by growth of some of the surrounding cells of the tissue as to bring about the change in position of the cell plate. The most obvious significance of the shifting of the cell plate is that the original position of the spindle cannot always be taken to determine accurately the ultimate plane of division of the cell.

CONCLUSIONS.

1. The most obvious and at the same time most important conclusion to be derived from the foregoing observations is that the division of the cell body is due to the activity of the kinoplasm of the cell. The splitting of the cell plate, or at least its differentiation into separate layers, is in the higher plants the essential act in the division of the cell body, for it is not until such a differentiation has taken place that there is a separation of the protoplasm of the mother cell into two distinct parts. That the cell plate is kinoplasmic has already been

[39] Ueber Kern u. Zelltheilung bei *Solanum tuberosum*. Flora **86**: 214. 1899.

insisted upon by Strasburger in two of his recent papers.[40] The difference between Strasburger's observations and mine is that in the former only a small portion of any one fiber is used in the process of cell plate formation, while in the latter the substance of the whole fiber becomes transformed into a portion of the cell plate, *i. e.*, in the one case the cell plate is simply a product of the activity of the kinoplasmic fibers, the fibers themselves not being used in the process, while in the other case the cell plate is a result of a change of form of the substance composing the fibers. The identity in character of the substance of the cell plate and that of the spindle fibers has an important bearing on the relations of the different methods of cell division occurring in different groups of plants. The process of free cell formation in the embryo of Ephedra, as described by Strasburger, is an interesting case of kinoplasmic activity, in which the division takes place around a single nucleus instead of between two nuclei as in regular cell division. The fact that the membranes are formed simultaneously would show that this process goes on around all parts of the nucleus alike. It might be contrasted in this respect with the formation of ascospores, as described by Harper, in which the growth of the membrane is a progressive one and the nucleus is consequently modified in form to suit the necessity of kinoplasmic activity from one point alone. The method of division of the egg from the endosperm mother cell and the synergids, as described by Mottier[41], presents a process intermediate between the method of free cell formation in Ephedra and that of regular cell division. Here, where there are two nuclei lying adjacent to one another, the cell plate is formed in connecting spindles between them, but where, as in the case of one synergid in Mottier's *fig. 22*, the fibers end blindly in the cytoplasm, a cell plate is formed in such fibers, following the method of Ephedra. In all of the above cases the formation of a membrane from the fibers is an established

[40] Ueber Cytoplasmastructur und Zellhäute.

[41] Ueber das Verhalten der Kerne bei der Entwickelung des Embryosacks und der Vorgänge bei der Befruchtung. Jahrb. f. wissen. Bot. **31**: 123. 1898.

fact. The method of cell division by constriction of the plasma membrane, which occurs in many filamentous algæ, may be analogous to the growth of the plasma membrane as the cell increases in size, with the difference that in the former case the growth of the plasma membrane is localized and proceeds without the accompanying growth of the cell contents.

2. I have already indicated what seems to me to be the relation of the nucleus to the kinoplasm in the process of cell division. It is the center of the metabolic processes concerned in the production of the kinoplasm. Whether there is a transformation of some previously existing substance of the cell into the filar form of kinoplasm I have not been able to determine. From the two facts that no such transformation is visible and that a great many of the fibers are used up in the formation of a membrane, I think it probable that they are formed anew in each cell. That the chromatin is the real center for their formation is shown by the formation of new radiating fibers around the daughter nuclei in the onion during the diaster stage, and by the formation of a spindle around a single chromosome in the manner described by Juel for Hemerocallis. The history of the kinoplasm in a single cell of the higher plants would seem to be as follows. It is formed as fibers around the nucleus as a center. In this form the kinoplasm takes part in the process of nuclear division, and later divides the cell by a part of the fibers being transformed into a membrane which becomes in splitting the plasma membranes of the daughter cells.

In cases where cell division does not follow immediately upon nuclear division the filarplasm may be absorbed into the general protoplasm of the cell, either to reappear or to be formed anew when needed for cell division. The ultimate form of the kinoplasm of any one cell seems to be reached when it has become a plasma membrane. It is then concerned with the activities of the resting cell. The transformation of kinoplasm from the filar into the membrane form seems to show that the hypothesis of a permanent substance, which may be described

by the term "filarplasm," lately proposed by Strasburger,[42] is not well founded. To be sure there are, in a great many cells, spindle fibers that seem to take no part directly in the formation of membranes, but they apparently lose their filar form. The most permanent form of the kinoplasm seems to be of the membrane. It would seem better, then, to retain the older physiological term kinoplasm, since such a term would denote a substance having certain physiological properties without necessarily being limited to any one form. The conclusion reached by Kostanecki[43] of the permanency of the spindle fibers in the cell, and that they are always reproduced by division of the individual fibers, "omnis radius e radio," is, as Nemec[44] has pointed out, unsupported by the history of the fibers in plant cells. It would be impossible, moreover, to account thus for the manner in which the fibers are transformed into a membrane.

3. The relation of the carbohydrate material to the process of division would seem to show, as already stated, that the substance for the formation of the cell wall is held in a reserve form in the protoplasm before it is actually needed for the process of wall formation. The fact that it appears in connection with the spindle would suggest, as Farmer and Williams have shown, that the spindle fibers have for their substance a conductive function. These authors did not ascribe a formative function to the fibers because they did not find any cell plate. It is not impossible that the cell plate may have been entirely overlooked in this case. In some of my own preparations it was often very difficult to discover the young cell plate in the midst of the carbohydrate material.

If the above mentioned relation of the carbohydrate material to the spindle be taken in connection with the facts shown by Klebs,[45] and by Townsend,[46] that the presence of a nucleus is

[42] Zellhäute. [43] *Op. cit.* [44] Kerntheilung von *Allium Cepa*, 321.

[45] Beiträge zur Physiologie der Pflanzenzelle. Untersuch. a. d. botan. Institut z. Tübingen **2**: 500. 1888.

[46] Der Einfluss des Zellkerns auf Bildung der Zellhäute. Jahr. f. wissen. Bot. **30**: 484. 1897.

necessary for the formation of a cell wall, there would be some evidence for the hypothesis that the nucleus forms the cell wall substance.

The investigations described in the foregoing pages were begun at Lake Forest University under the direction of Professor R. A. Harper, whose helpful interest and valuable criticism have continued throughout their progress. The work was continued and practically completed in the botanical laboratory of the University of Michigan during the years 1897–8 and 1898–9. I wish here to thank Professors Spalding and Newcombe of the above laboratory for the liberal way in which material and equipment were provided, and for many helpful suggestions received. Professor Jacob Rheigard, of the department of zoölogy of the University of Michigan, very kindly allowed the use of the photographic apparatus of that department, and Dr. J. B. Johnston aided me greatly in making the photographs.

THE UNIVERSITY OF WISCONSIN.

EXPLANATION OF PLATES VIII AND IX.

Figs. 1–21 are reproductions of photographs made with the Zeiss photomicrographic apparatus. (Figs. 9 and 22 have been purposely omitted.) Figs. 23–31 are from drawings made with the aid of the camera lucida, Zeiss 2^{mm} immersion objective, and compensation oculars 8, 12, and 18. The size has been reduced $\frac{1}{3}$ in reproduction.

Figs. 1–10. *Larix;* pollen mother cells.

FIG. 1. Equatorial plate. × 750.

FIG. 2. Early diaster showing first stages in preparation for cell plate formation; the central spindle is differentiated into three zones. × 1200.

FIG. 3. Later than preceding; central spindle alike throughout. × 1200.

FIG. 4. Cell plate elements just forming. × 1200.

FIG. 5. Young cell plate has begun to grow in area; connecting fibers are beginning to disappear. × 1200.

FIGS. 6–10. Later stages in the growth of the cell plate; see explanation in text. × 1200.

FIGS. 11–21. *Allium Cepa;* cell of growing root-tip.

FIG. 13. Equatorial plate; spindle fibers arranged into strands or bundles. × 1500.

FIGS. 14–15. Metaphases showing granular appearance of region between the groups of daughter chromosomes. × 1500.

FIG. 16. Stage corresponding to *fig. 2*. × 1500.

FIGS. 17–19. Later stages showing the equatorial zone containing carbohydrate material. × 1500.

FIGS. 18–19. Formation of cell plate in the midst of the zone of carbohydrate material. × 1500.

FIGS. 20 and 21. Growth of cell plate and disappearance of spindle fibers. × 1500. See also *fig. 11*.

FIGS. 12 and 21. Stages showing change of position of cell plate from a diagonal to a transverse position. × 1500.

FIG. 23. *Larix;* showing arrangement of spindle fibers and differentiation of cytoplasm into layers. × 3000.

FIG. 24. *Larix;* details in relation of radiating fibers to the connecting fibers in a stage represented by *fig. 3*. × 4500.

FIG. 25. *Allium;* portion of spindle in late metakinesis, showing relations of fibers to one another and distribution of granules in the spindle. × 4500.

FIG. 26. *Larix;* two radiating fibers lying adjacent to the central spindle and crossing in such a way as to appear fused. × 4500.

FIG. 27. *Larix;* different stages in the transformation of the substance of a spindle fiber into a portion of the cell plate. × 4500.

FIG. 28. *Allium;* relation of the connecting fiber to the carbohydrate material at the equator. × 3000.

FIG. 29. *Allium;* cell plate elements formed on the connecting fibers in the midst of the carbohydrate material. × 3000.

FIG. 30. *Allium;* late stage in the growth of the cell plate, showing the relation of the outer radiating fibers to the growing portion of the plate. × 4500.

FIG. 31. *Allium;* cell plate with young cell wall showing in the cleft where the cell plate is split. × 3000.

ERRATUM: on p. 85, line 16 from top, *fig. 10* should read *fig. 13*.

PHYSIOLOGICAL OBSERVATIONS ON SOME PERENNIAL HERBS.

A. RIMBACH.

(WITH PLATE XIII)

I.

Arisaema Dracontium (L.) Schott.—During winter *Arisaema Dracontium* consists of a stem-tuber, the growing point of which, covered by several scale leaves, lies at about 5^{cm} below the surface of the earth. It is devoid of roots. Early in April the bud begins to elongate upwards, and at the same time from fifteen to thirty roots break out in a ring like zone from the base of the bud (*fig. 4*). They appear almost simultaneously and grow horizontally, radiating in all directions from their point of origin. They are 1 to 1.5^{mm} in diameter throughout their entire extent, and attain a length of more than 20^{cm}. After a time some of them become somewhat transversely wrinkled at the base, because they undergo there a slight longitudinal contraction. At the end of April the scale leaves protrude from the soil. They are tightly appressed to each other and enclose a hollow, in which the foliage leaf develops (*fig. 6*). In the latter the end leaflet is vertically extended, the lateral leaflets are bent downwards, and the blades of all are involutely rolled up. After having reached the surface of the earth, the scale leaves stop their growth, and at the end of April or beginning of May the foliage leaves and inflorescences break out from their coverings and unfold in the air. In the course of May the inflorescence opens. About the same time a second set of roots is formed immediately above the first one (*fig. 5*), but there is a striking difference between the two. The roots of the second set are thicker, about 2.5^{mm} in diameter, and taper towards the end. They grow from their origin vertically downwards or nearly so, and pass over into a horizontal direction only at their thin end

portion. They undergo very soon a considerable longitudinal contraction in the thickened basal portion, which is usually 2 to 4^{cm} long. After having attained a certain intensity, this contraction manifests itself externally by a shriveling of the root surface. I noticed, however, that these roots of the second set are not in all individuals developed in the same degree. In specimens, for instance, which were located at a considerable depth, these roots differed very slightly from those first formed. On the other hand, in individuals which were placed very superficially I found the roots exceptionally thick and exceedingly numerous.

The contraction amounts to about 40 per cent. within the space of 5^{mm} in the swollen basal portion. It diminishes in intensity towards the thin terminal portion, where no contraction at all takes place. The whole contraction of the root amounts to about 15^{mm} or even more, the contractile region having originally an average length of about 5^{cm}. Of these facts I satisfied myself by marking and measuring the roots during their development in the earth. For this purpose the plants were cultivated in specially constructed culture-cases, furnished with lateral windows, which could be removed thus permitting access to the roots. The active contractile tissue is here, as in other roots of similar structure, the cortical parenchyma. The central axis of vascular bundles with the endodermis is passively contracted, and the same holds good for the epidermis and exodermis and one or two layers of parenchyma immediately below the latter. These passive layers of the outer cortex very soon become folded, and form transverse wrinkles. During contraction, which process lasts in the whole root about three or four weeks, the shortening cortical parenchyma cells elongate very much radially. The root, however, does not grow in diameter, but the outermost layers of the active parenchyma after a time collapse and become tangentially compressed by the inner ones, so that finally a rather wide area of crushed cells is found surrounding a few layers of the still turgescent innermost cells. In the endodermis, as well as in the exodermis, there is also a remarkable

result of the root contraction noticed. The radial longitudinal walls of their cells, being quite straight at the beginning, as contraction sets in become marked with wavy foldings. In the endodermis the waves are strongest in that longitudinal band of the wall which corresponds to the well-known dark spot on the cross-section.

As each root is fastened at its tip to the earth and at its base to the tuber, in consequence of the contraction a tension is set up in it, and the root must give way at the point less firmly fixed. As a matter of fact, mostly the base of the root moves towards the tip and pulls the tuber with it. Thus, by the combined action of all the roots, since all in their basal part point steeply downwards and differ but little in direction, the tuber is drawn down into the earth a certain amount every year.

Thus the contractile roots determine to a great extent the position of the tuber. The latter is found sometimes upright, sometimes lying horizontally, not seldom even turned over with the bud directed downwards, so that the leaf-stalks and stems have to make a strong curvature in order to attain an upright position. The situations are largely due either to a uniform or one-sided pull of the roots. I am not able to say with certainty which direction of growth the tuber would take up by itself, and whether its behavior in this respect would be the same under different external conditions. The annual prolongation of the tuber is in larger individuals from 6 to 10^{mm} (*fig. 6*), and if the tendency of growth were always upright, the dragging action of the roots would of course be of essential importance for keeping the growing point in place and preventing its emerging from the earth.

All the roots are furnished with root-hairs, and form later a few branches of the first order in their terminal portion. At the time of the withering of the leaves all the roots die off, and their scars are then found in a ring-like zone on the surface of the tuber (*sc*, *fig. 4*).

In the axils of the scale leaves lateral buds originate, four or five every year, which persist after the leaves which support

them have disappeared, and are found in the fall of the same year as lateral protuberances upon the fully developed portion of the tuber (*bd*, *fig. 6*). During the next spring they enlarge considerably, and later, as that portion of the tuber on which they are inserted becomes emptied and dies off, they are set free. As a rule, they do not yet develop a leaf and roots in the same year, but remain dormant and sprout only in the second year after that in which their supporting leaves were vegetating. The tuber always contains but one year's growth in a fully developed state.

The leaves and roots perish in July or August, and soon after the berries ripen. During the germination of the seed, which takes place in the following spring, the cotyledon, growing downwards, elongates so much that the growing point of the stem of the seedling is located 8 to 10^{mm} below the seed (*fig. 1*). The upper end of the cotyledon, which remains in the seed, swells up so as to form an ellipsoid sucker, which finally becomes about 5^{mm} long and displaces in part the emptying endosperm. While this is taking place the first foliage leaf sprouts out and penetrates the earth with a knee-like nutation of its stalk (*l*, *fig. 1*). Already the first root of the seedling, reaching 3–5^{cm} in length and 0.75^{mm} in thickness, is a little contractile at its base, although it does not become wrinkled. During the subsequent development the little stem of the seedling swells up, chiefly below the insertion of the cotyledon, forming a little tuber; out of the latter, during the first year, two, or mostly three, seldom four, adventitious roots are formed (*fig. 2*). Each one of these grows longer and thicker than its predecessor, and develops also a longer contractile region. The fourth root, for instance, is usually about 10^{cm} long and 1.5^{mm} thick; its contraction amounts within the space of 5^{mm} to 40 per cent.; its total contraction amounts to about 10^{mm}. I observed in various specimens that by the work of the roots the little tuber was drawn down from 8 to 10^{mm} during the first vegetative period. So we find, at the end of the first period of growth, the terminal bud of the plant from 15 to 20^{mm} deeper than it was located

in the seed before germination (*fig. 3*). In the following years this migration of the plant downwards continues in a similar way. The alternation of roots mentioned above shows itself from the second year onward.

While the occurrence on one and the same plant of two kinds of roots differing in form and function is not very rare, the formation of these at different times, as in Arisaema, has so far been found only in a few species. I have noted the same fact, for instance, in *Allium ursinum* L., *Fritillaria Meleagris* L., *Scilla bifolia* L., and some other monocotyledons.

Arisaema triphyllum (L.) Torr. resembles perfectly *A. Dracontium* in the behavior of the underground organs.

The contraction of the roots seems to play a great part in another American species of Araceæ, in *Spathyema foetida* (L.) Raf. In this plant a stem-tuber is formed, which grows vertically upwards, dying off gradually at its lower end. This tuber attains 10^{cm} in length and 5^{cm} in thickness, and comprises the products of several years. It forms yearly about fifteen roots near its upper end. These grow obliquely downwards, tapering toward the tip, and produce from their thin end portion lateral rootlets of the first and second orders. They live several years, so that about sixty to seventy of them are found in one plant. All the roots are contractile, and apparently prevent the emerging of the tuber from the ground. This has been assumed also by Foerste, who found the seedlings germinating within an inch of the surface of the ground and the top of the root stock several inches below the surface. I found the seeds germinating on the surface of the soil and the growing point of the tuber in several larger specimens at a depth of about 10^{cm}.

Just the same phenomenon may be observed in *Hypoxis hirsuta* (L.) Coville. This plant also has an upright growing stem-tuber attaining 3^{cm} in height and 2^{cm} in diameter. All its roots, which start from it in a ring-like belt, are more or less contractile in their thickened basal portion, which becomes transversely wrinkled, and as they grow steeply downwards they are enabled

to drag the tuber vertically into the ground. I found the growing point of older specimens mostly in a depth of 3^{cm}.

In *Trillium sessile* L. I found most of the roots possessing a strongly contractile swollen basal portion, which soon becomes wrinkled. In this species the tuber very often by the power of the roots is drawn into a horizontal or even downwardly directed position.

Mesadenia tuberosa (Nutt.) Britton, a composite growing on wet places of the prairie, has a stem-tuber about 2^{cm} in length, which yearly grows from 10 to 12^{mm} vertically upwards, while it dies off in the same proportion at its lower end (*fig.* 7). The tuber comprises the products of two years, separated by a constriction. Every new member of the tuber, in May after its formation, sends out about twelve roots, originating in a simple ring. These roots grow obliquely downwards and attain a length of more than 30^{cm}. They are at the beginning about 2^{mm} thick, but grow secondarily in thickness, attaining at least a diameter of 4–5^{mm}. They exhibit considerable contraction, and pull the stem as much back into the ground as it elongates upwards. The roots seem also to show reserve material. They persist through two vegetative periods and form later numerous long but very thin lateral rootlets, branching sparingly in their turn. There is a vegetative multiplication by lateral buds, which become isolated by the decay of the mother tuber.

The species of *Arisaema*, *Spathyema*, *Hypoxis*, *Trillium*, and *Mesadenia* mentioned above can therefore be classed together in one group, characterized by possessing a rhizome growing more or less vertically upward, which becomes drawn down by contractile adventitious roots. To the same group belong also the following species: *Hyacinthus candicans* Baker, *Lilium Martagon* L., *Allium ursinum* L., *Succisa pratensis* Moench, and *Plantago major* L.

II.

Erythronium albidum Nutt.—During summer the bulb of *Erythronium albidum* lies hidden in the earth without aerial organs and without roots. I found the growing point of flowering bulbs,

of which I examined about twenty-five specimens in the month of April, mostly between 15 and 16^{cm} distant from the surface of the earth, the extreme cases being 11 and 20^{cm}. The sterile specimens, the bulb of which as a rule is smaller, were encountered always at a less depth. Of the about 200 specimens of this latter kind which I examined, the larger ones were found at an average depth of 9.5^{cm}, the extremes being 5 and 15^{cm}, and the smaller ones at an average depth of 7.5^{cm}, the extremes being 4 and 13^{cm}. I took into consideration only those individuals which were found on an even ground and apparently had not suffered any considerable disturbance. Hence the smaller plants, as a rule, are found in a more shallow position than the larger ones.

In the late fall—the exact time I am unable to give—the roots break out from the stem portion of the bulb. They appear all at once, their number being in the smallest specimens from four to ten, in the largest from twenty to forty. They are about 0.75^{mm} thick, uniform throughout, become about 15^{cm} in length, and never branch. In the specimens I examined root hairs were not present. These roots do not exhibit any contraction. Their direction of growth varies very much, and seems to be largely influenced by local factors.

At the beginning of April the leaves emerge from the ground, penetrating the earth with the cartilaginous point of the erect inwardly convolute blade. The young specimens develop only one leaf, the older ones a stem with two leaves and with or without a flower. With the development of the aerial organs the emptying of the old bulb-scales and the formation of a new bulb begin. The new bulb may be formed close to the old one, or may be removed from it to a more considerable distance by means of a runner. Of 200 sterile individuals I examined, 114 had formed a runner, the rest not, and of 25 flowering individuals only three had formed runners.

The runner is solid in its basal half, but in its terminal half it contains a narrow, longitudinal channel, the termination of which on the surface is found usually a little below the middle of its

length on the side opposite the roots. In those sterile specimens which do not form a runner the corresponding opening is found on the same side of the bulb at the base of the foliage leaf, about 5^{mm} from the roots upwards. In both cases the opening leads to a hollow space, near the end of which the new bulb is formed. In the sterile individuals mostly two runners are formed by each bulb, the one being about twice as long as the other and also thicker. The longer runner reaches an average length of about 12^{cm}, with a diameter of $2–3^{mm}$, the longest I found being 17^{cm} in length. In flowering specimens I found the runner $3–5^{mm}$ thick and 8^{cm} long, but I do not know the definite length it may attain. Where the new bulb is formed close to the old one, one finds instead of the smaller runner only a little bud. The smaller runner, as well as the little bud mentioned, may be found sometimes at the right, sometimes at the left side of the main bulb.

Without entering into morphological considerations about the parts of stem and leaves which take part in the formation of these structures, we will consider only their physiological behavior. At the end of April the elongation of the runner stops, and the new bulb enclosed in its point begins to swell up. At this time the old bulb-scales are completely emptied, but starch grains are found in the whole extent of the runner and in large quantity in the new bulb. During May the development of the new bulb is accomplished, and at the end of the month the foliage leaves, the old bulb, and the runner die off, so that at the beginning of June the new bulb is isolated. It remains in a dormant state until the fall of the same year, when the above described cycle recommences.

The difference between those specimens which separate the new bulb from the old one by a long runner, and those which form it close to the old one, lies only in the relative length of the stalk uniting the stout stem-portions of the two bulbs. Those stem-portions in which the leaves are inserted and from which the roots start are rich in vascular bundles, and their remnants may be preserved several years. Sometimes two, three,

or four of them are found still attached to a bulb, indicating the places where the plant had rooted in former years. In case no runner is formed, the bulb advances from 2 to 6^{mm} every year, this being the distance of the points of rooting of the subsequent bulbs. Through the formation of a runner, the distance of the subsequent bulbs amounts to 3 to 10^{cm}, being as a rule somewhat smaller than the length of the runner, as the latter usually is curved.

By the growth of the stalk uniting the subsequent bulbs, whether this stalk be short or long, the plant may suffer a dislocation both in horizontal and vertical direction. In both cases the position of the rhizome is somewhat singular, the side from which the roots are formed being turned upwards, and the side on which the bud arises downwards. Where a short stalk is formed, it is directed obliquely downwards and advances the plant a few millimeters in this direction. Where a runner is developed, it grows horizontally at the beginning, but later turns more or less vertically downwards, thus placing the new bulb several centimeters lower. I found in an examination of about 100 specimens the new bulb of the main runner on an average 4.6^{cm} deeper than the old one, while the bulb of the smaller runner was sunken but half as deep. The extreme cases of sinking observed in the larger runner were 1^{cm} and 10^{cm}, in the smaller one 0^{cm} and 6^{cm}. In full-grown flowering specimens a runner seems to be formed but rarely, as I found in most of them the remnants of several years' growth close to the actual bulb, the plant advancing horizontally about 6^{mm} every year. But the young, small individuals also, even in a rather shallow position, do not form a runner every year. Specimens of this latter kind which I found had formed no runner during three years; others, which had developed a runner this year, had been devoid of it in the preceding year, as was shown by the remnants of the last year's bulb; others, furnished with a runner the present year, seemed to have formed one also in the foregoing year, since not the slightest indication of an old bulb was present in their neighborhood.

I do not know what rule may exist in this alternation or by what factors the formation of a runner may be determined. Nevertheless, from my notes it seems that a shallow position of the plant favors the development of a runner. Probably all the shallow, small individuals are derived from seedlings, germinated near the surface of the soil. Their mode of growth must bring them gradually into the depth of the full-grown individuals. By the yearly duplication of their bulbs a rapid vegetative multiplication takes place.

Erythronium mesachoreum Knerr.—This plant, which resembles *E. albidum* very much, inhabits the open prairie. I found the growing point of the bulb in about twenty-five full-grown individuals which I examined between 9 and 13^{cm} distant from the surface of the earth, the average depth being about 11^{cm}. In this species the small, sterile individuals occupy a more superficial position, being found at a depth of from 3 to 8^{cm}. They apparently have originated from seeds. In the early part of April the formation of the new bulb begins. In the young shallow individuals I always found the new bulb removed from the old one by a runner, but the latter is short, the longest I saw being about 20^{mm} in length, and it grows from the beginning vertically downwards, thus placing the plant every year from 3 to 20^{mm} deeper (*fig. 8*). In this species I never noticed the formation of more than one runner by one bulb. The result of this manner of growth is that the formations of the subsequent years are arranged in a vertical row, and I found, in fact, the remainders of the products of five years located in this way above the living bulb; the leaf of the present year making its way through the long channel formed by all the dead integuments (*fig. 9*). By such a movement of growth the plant finally reaches a depth beyond which it does not advance. I found, indeed, that in the old full-grown individuals, situated at a depth of about 11^{cm}, the bulb grows no longer downwards, but horizontally or nearly so, the new bulb rooting about 4^{mm} laterally from the old one.

The observations on *Erythronium mesachoreum* as well as *E. albidum* were made in the neighborhood of Lincoln, Neb.

So far as the physiological behavior of the rhizome and roots is concerned, *Lilium superbum* and *Medeola Virginiana* agree almost perfectly with *Erythronium*.

Lilium superbum L. has a horizontal rhizome, in which stem and leaves are fleshy, and participate in the same degree in the storing of reserve material. Each year's growth of the rhizome is in full-grown specimens about 4^{cm} long, forming at first a runner-like stem portion beset with a few small fleshy scales, and at last a stout, bulb-like structure with numerous crowded fleshy scales, from the middle of which the aerial stem arises. From the under side of this terminal bulb-like portion of the rhizome, just at the place where the aerial stem originates in June, about ten thin roots grow out horizontally, radiating towards all sides and sparingly forming lateral branches of the first order. They do not exhibit any contractility, and last but one year, the rhizome dying off from behind very quickly. I found the growing point of the rhizome in full grown specimens between 7 and 10^{cm} below the surface of the earth. The plant must reach and keep this depth, as the roots are quite inactive, by the movement of growth of the rhizome itself. This behavior, which some other American species of Lilium seem to share, is entirely different from that of *Lilium Martagon* and other species of the Old World, in which the bulb grows vertically upwards, and is drawn down by strongly contractile roots.

Medeola Virginiana L. has a horizontally creeping tuberous rhizome, representing but one year's growth in the fully-developed state. The hibernating, tuber-shaped, end portion of the rhizome bears about twenty or twenty-five thin, thread-like roots, which attain 15^{cm} in length and produce numerous branches of the first and a few of the second order. These roots are not contractile, and radiate in all directions from the rhizome, meandering very much in their course. On even soil I found the rhizome growing in a depth varying from 1 to 4^{cm}. Also here the movement is due to the rhizome alone, the roots taking no part in it.

The roots of *Erythronium albidum* and *E. mesachoreum*, *Lilium superbum*, and *Medeola Virginiana* have only a nutritive function. They are of no great importance in fixing the plant in the earth, nor do they exert any strain upon the parts from which they start, nor do they store any considerable quantity of reserve material. In contradistinction to those of Arisaema, Spathyema, Trillium, and Hypoxis, we find in these roots but little cortical parenchyma, no compressed cortical cell layers, no wrinkling of the root surface, and a total absence of wavy foldings in the longitudinal walls of their endodermis and exodermis. The species of Erythronium, Lilium, and Medeola above mentioned are representatives of a type of geophilous plants in which the rhizome, by its manner of growth, seeks and keeps a certain depth in the ground, without any help of the roots. *Dentaria bulbifera* L., *Paris quadrifolia* L., *Colchicum autumnale* L., *Orchis mascula* L., and *Platanthera montana* Reichb. f. are species which belong to the same type.

III.

Many perennial herbs develop a long tap root, which becomes more or less thick and fleshy, and filled with reserve material. To this group belong the following species: *Kuhnia eupatorioides* L., *Lacinaria punctata* (Hook.) Kuntze, *Grindelia squarrosa* (Pursh) Dunal, *Nothocalcis cuspidata* (Pursh) Greene, *Kuhnistera candida* (Willd.) Kuntze, *K. purpurea* (Vent.) MacM., *Psoralea esculenta* Pursh, *Astragalus crassicarpus* Nutt., *Peucedanum foeniculaceum* Nutt., *Callirrhoë alceoides* (Michx.) A. Gray, *Delphinium Carolinianum* Walt., *Aquilegia Canadensis* L., *Asclepias tuberosa* L., *Lithospermum angustifolium* Michx., *Physalis longifolia* Nutt., and *Allionia nyctaginea* Michx.

In many of these plants the contractility of the root is an important feature. I have noted this phenomenon in *Allionia nyctaginea*. In seedlings of this plant it can be observed easily that the base of the cotyledons, which at the beginning finds itself above the ground, after some weeks disappears under the surface of the earth. That this is really due to the contraction of the root I satisfied myself by marking the root of young

specimens, grown in a special culture case, from their base with lines of India ink 5^{mm} apart. These 5^{mm} spaces shortened to 4^{mm} each within six weeks, which equals a contraction of 20 per cent. At the same time the uppermost line, that next the root base, moved about 6^{mm} downwards, placing the base of the shoot so much deeper.

Also in *Aquilegia Canadensis* I observed a considerable shortening of the root, which results likewise in drawing down the growing point into the earth. In seedlings of *Aquilegia vulgaris* L. I noticed that the growing point of the stem, which immediately after germination stood 8^{mm} above the ground (*fig. 11*) was found at the end of the first summer, in consequence of the contraction of root and hypocotyl, about 6^{mm} below the surface of the earth (*fig. 12*). The upper lateral roots become bent down during this process in a very characteristic manner, (r^1, *fig. 12*). The transverse wrinkling of the surface in the older roots of Aquilegia and Allionia is due to the same cause, and corresponds to the folding of the roots of Arisaema, Hypoxis, and others.

There can scarcely be any doubt that in *Lithospermum angustifolium*, *Nothocalcis cuspidata*, *Peucedanum foeniculaceum*, *Astragalus crassicarpus*, *Kuhnistera candida*, and *K. purpurea* the root is also contractile, although I have not had the opportunity to measure it directly. This seems to be indicated by the following points: the undulating course of the innermost vascular bundles, the transverse wrinkling of the outer bark, the disturbed position of the upper lateral roots, and finally the position of the growing point below the surface of the earth, in spite of the continual prolongation of the perennial stem-portion towards above. Also in *Kuhnia eupatorioides* and *Grindelia squarrosa* contraction seems to occur, although in a less degree, while in *Lacinaria punctata* it possibly may not exist at all. In pieces of roots of *Lithospermum angustifolium* and *Kuhnia eupatorioides* lying in water, I observed after two days a considerable shortening.

In addition I might say something concerning *Lacinaria squarrosa* (L.) Hill, which, although resembling *L. punctata* very

much in its aerial organs and even in its germination, differs considerably in the development of its underground organs. *Lacinaria squarrosa* has an underground roundish tuber about 3^{cm} high with four lateral swellings, a partition that seems to correspond to the tetrarchic arrangement of the vascular bundle in the primary root. I am not able to say, however, whether the tuber is formed only by the basal portion of the primary root, or whether the hypocotyl also or the stem take part in it. At all events, the terminal portion of the main root does not persist, but is replaced by new lateral roots starting from the tuber. Those roots originate in the older plant in four groups of from five to fifteen situated on the four swellings of the tuber (*fig. 13*). They break out from the tuber all at once in the latter part of April at the time when the first leaves appear. They are white, soft, somewhat thickened in their basal portion to an extent of 2 or 3^{cm}, attaining here a diameter of 2^{mm} and tapering very rapidly to a diameter of only 0.5^{mm}. They grow at the beginning almost vertically downwards, reach about 50^{cm} in length, and form very thin branches of the first and second orders, with numerous long root-hairs. The thickened portion of the root consists at the beginning mostly of soft, thin-walled tissue and is contractile, exhibiting according to my measurements in the culture case a shortening of 6–10 per cent. within a space of 5^{mm}. The whole root probably never shortens more than from 2 to 4^{mm}. The contraction ceases after four or five weeks of growth of the root, and during this time the characteristic wavy foldings in the walls of the endodermis and exodermis make their appearance. Later the root becomes more rigid on account of the development of thick-walled cells in the central axis. At the beginning of October, when the fruits are ripe and the aerial shoots begin to die, the roots perish, and during winter there are no living roots on the plant. In old specimens of *Lacinaria squarrosa* the roots probably cannot produce a movement of the tuber, while in younger plants it possibly might happen. But they help apparently to hold the plant in place by the strain hey exert. This contrivance seems to be useful, since

perennial organs of attachment are wanting, and since the tuber is very superficially located and the aerial shoot is relatively high, heavy, and exposed to strong winds.

Physalis longifolia Nutt. does not show any contraction of its long fleshy tap root, but reaches a considerable depth in quite another way. The plumule of the seedling is raised 5 to 10^{mm} above the ground and transforms itself afterwards into a long shoot. The primary root grows vertically downwards, sending out numerous thin lateral rootlets, and becomes subsequently thick, fleshy, and filled with starch. Very soon on its surface adventitious buds appear, some at the upper end at the limit of the hypocotyl, rarely on the hypocotyl itself, others deeper down at a distance of 6 or 8^{cm} from the surface of the earth. At the close of the vegetative period the upper part of the plant dies down, but the root, at least a part of it, with its buds, hibernates, and at the beginning of the next year one or more of the buds, now much deeper than the plumule was, grow out by means of the reserve material stored up in the root. In older specimens I found the root 1^{cm} thick and extending to a depth of more than 50^{cm}.

The seedling of *Asclepias Cornuti* Decne shows a development of root shoots quite similar to that of *Physalis longifolia*.

Delphinium Carolinianum, *Callirrhoë alceoides*, and *Nothocalcis cuspidata* are distinguished by the peculiar phenomenon that in older specimens the root is slit into several longitudinal cords in consequence of the dying off of certain tissue portions. I found the root of Delphinium, for instance, divided into eight cords, forming a circle round a central hollow space and connected above and below. In Nothocaleis the root at a length of 12^{cm} becomes variously pierced and divided into two, three, or four longitudinal cords, each of them about 6^{mm} thick, united lattice-like at different heights. This fission of the root is not caused by simple decay of the older tissue, but is due to a peculiar mode of growth in thickness. The details of the processes concerned deserve closer study. A corresponding phenomenon has been observed and studied by Fost in *Gentiana cruciata* L.,

Corydalis nobilis Pers., *C. ochroleuca* Koch, *Salvia pratensis* L., *Aconitum Lycoctonum* L., and *Sedum Aizoon* L. I observed it in *Scabiosa arvensis* L. and saw a fission into four cords also in the subterranean stem of *Gentiana puberula* Michx.

In addition, I have noticed in *Nothocaleis cuspidata* a daily opening and closing of the flower heads. My observations were made between May 1 and 15, in sunny, moderately warm, windy weather on the prairie near Lincoln, Nebraska, where this plant grows naturally. The heads begin to open at 7 A. M., and are at 9 A. M. fully expanded. They remain so till 3 P. M., at which time they begin to close again. At 4:30 P. M. they are all closed, and they stay so during the night.

All the plants mentioned, furnished with a deep tap root, are confined to the place they occupied when germinating. Besides, they lack vegetative multiplication, their only means of propagation being by seeds. Perennials of this type are exceedingly numerous on the prairie. Nevertheless, other forms occur also, like *Helianthus scaberrimus*, with long, horizontal rhizomes, by means of which they are enabled not only to change their place, but also to multiply vegetatively.

Helianthus scaberrimus Ell., as found in early spring, consists of a subterranean shoot 2 to 4^{cm} long, horizontal or ascending at its end, furnished with about twelve long rigid roots, directed obliquely downwards and forwards. At the end of April the terminal bud of the rhizome leaves out, forming immediately long internodes, the first of which bear scale leaves. In the middle of May, from the stem nodes between the roots and from the axils of the scale leaves above them, six to ten white runners start. These take up a horizontal direction and continue growing till August, attaining a length of from 50 to 100^{cm}. Like the leaves of the aerial stem, the scales of the rhizome are opposite, the youngest ones covering the growing point and protecting it during its way through the earth. The runner is 2 to 3^{mm} thick and consists of about twenty internodes, the longest of which may measure 8^{cm}. The last four or five internodes of the runner are very short, and this stout end-portion at the

middle of September gives rise to new roots, while its terminal bud, having stopped its growth, remains quiescent until next spring. At the middle of November, when the aerial shoot has died down, the runner begins to decay from its base, while the roots have reached a length of about 20^{cm} and are still growing. During winter the runner decays, only its end portion with the roots remaining alive, and the plant assumes again the form in which we find it in the spring.

LINCOLN, NEBRASKA.

BIBLIOGRAPHY.

DE VRIES, H. Ueber die Kontraction der Wurzeln. Landwirtschaftl. Jahrbücher **6**: 927. 1877; **8**: 474. 1879; **9**: 37. 1880.

WARMING, EUG. Om Skudbygning, Overvintring og Foryngelse. Naturhist. Forenings Festskr. Kjöbenhavn 1884.

Ueber perenne Gewächse. (Botan. Centralblatt. **18**: —. 1884.)

FOERSTE, AUG. F. The development of *Symplocarpus foetidus* (L.) Salisb. Bull. Torrey Bot. Club **15**: 154. 1888.

FOST, L. Die Zerklüftungen einiger Rhizome und Wurzeln. Bot. Zeitung **48**: —. 1890.

ARESCHOUG, F. W. C. Beiträge zur Biologie der geophilen Pflanzen. Acta Reg. Soc. Phys. **6**: —. 1896.

RIMBACH, A. Ueber die Lebensweise des *Arum maculatum*. Berichte d. Deutsch. Bot. Ges. **15**: 178. 1897.

Lebensverhältnisse des *Allium ursinum*. *Ibid.* **15**: 248. 1897.

Biologische Beobachtungen an *Colchicum autumnale*. *Ibid.* **15**: 298. 1897.

Die kontractilen Wurzeln und ihre Thätigkeit. Beiträge zur wissenschaftl. Botanik. **2**: 1. 1897.

Das Tiefenwachstum der Rhizome. *Ibid.* **3**: 177. 1898.

Ueber *Lilium Martagon*. Berichte d. Deutsch. Bot. Ges. **16**: 104. 1898.

Beiträge zur Physiologie der Wurzeln. *Ibid.* **17**: 18. 1899.

EXPLANATION OF PLATE XIII.

All figures are drawn from nature, and, with exception of *fig. 10*, are natural size. The horizontal dash-lines indicate the surface of the earth.

FIG. 1. Seedling of *Arisaema Dracontium* still in connection with the seed; *s*, seed; *c*, cotyledon; *l*, first leaf; *r*, first root.

FIG. 2. The same, near the end of the first period of growth, having developed all its roots; *t*, tuber; r^1, contractile adventitious roots.

FIG. 3. The same, in the resting state after the first period of growth.

FIG 4. Small specimen of *Arisaema Dracontium* in April, forming the first set of roots; r^1, thin roots of the first set; *sc*, scars from the roots of the preceding years.

FIG. 5. A similar specimen, in May, forming the second set of roots; r^1, thin roots of the first set; r^2, thick contractile roots of the second set.

FIG. 6. *Arisaema Dracontium*, leafing out; longitudinal section; *sc*, scars from roots of the preceding years; *sk*, remnants of the skin of tuber portions emptied in former years; *bd*, lateral bud; the shaded part of the tuber is to be emptied this year.

FIG. 7. Tuber of *Mesadenia tuberosa*, in May; longitudinal section; r^1, roots formed in the present year; r^2, roots formed in the preceding year.

FIG. 8. Young descending specimen of *Erythronium mesachoreum* in April, with the runner developed; *b*, bulb; *l*, leaf-stalk; *r*, roots; *R*, runner.

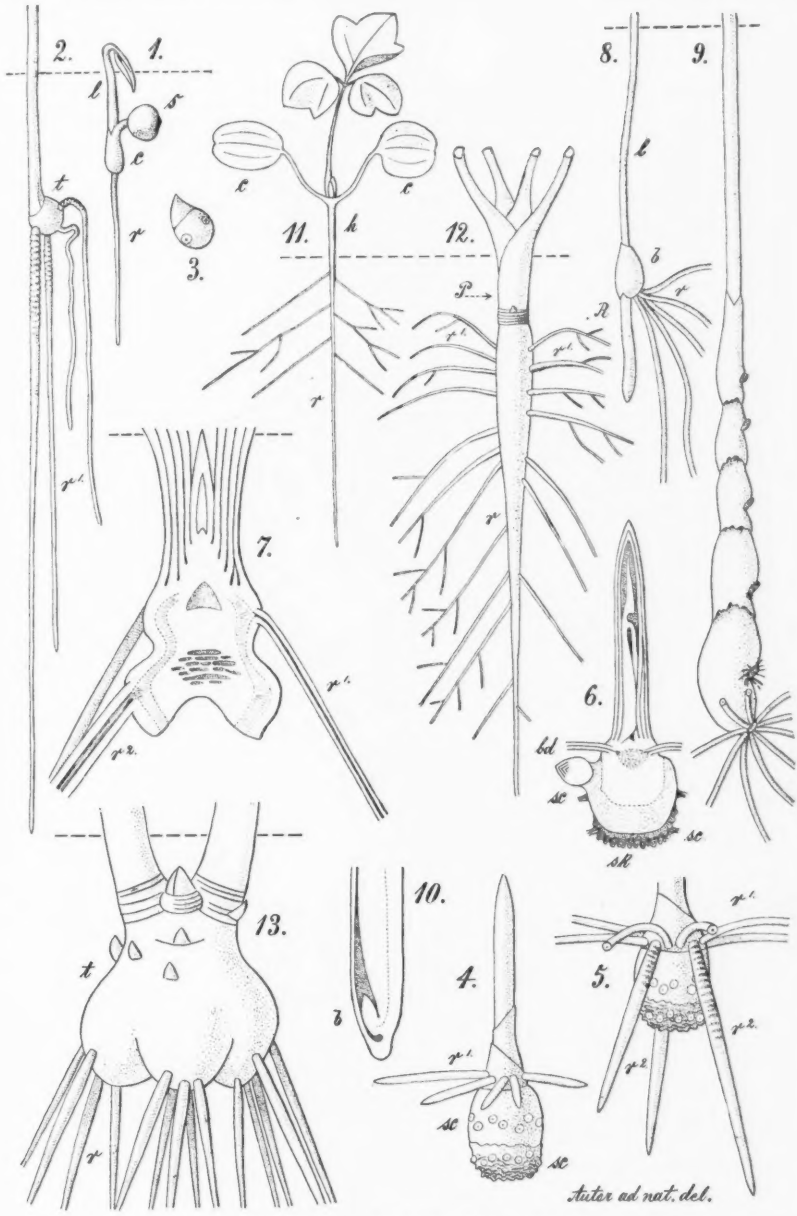
FIG. 9. Young sterile descending specimen of *Erythronium mesachoreum* with its remnants of the five preceding years.

FIG. 10. Tip of the runner of *Erythronium mesachoreum*; median longitudinal section; *b*, new bulb. × 5.

FIG. 11. Seedling of *Aquilegia vulgaris*, soon after germination; *h*, hypocotyl; *c*, cotyledons; *r*, primary root.

FIG. 12. The same, at the end of the first period of growth; *P*, place where the growing point is situated; *r*, primary root; r^1, lateral roots bent down by the contraction of the main root.

FIG. 13. *Lacinaria squarrosa*, subterranean part of a full-grown specimen in summer; *t*, tuber; *r*, contractile root.



RIMBACH on PERENNIAL HERBS

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. I.

AVEN NELSON.

Draba Yellowstonensis.— Annual, with stems of two kinds; the principal stem slender, erect, scape-like, 2–3^{dm} high including the raceme, simple or with long-peduncled racemes from the uppermost axil or axils; the one or more accessory stems from the base slenderer and shorter, ascending or erect: leaves mostly basal; root-leaves rosulate, from broadly linear to narrowly elliptic, sub-acute, entire or nearly so, 1–2^{cm} long; the few (2–4) stem leaves mostly near the base, narrowly ovate, generally smaller than the root-leaves; pubescence on the leaves finely stellate, on the stems and peduncles sparse, the hairs more or less branching: racemes long in fruit, usually more than half the whole height of the plant: pedicels shorter than the capsules: flowers small; the sepals elliptic, obtuse, about half as long as the petals; the petals cuneate-spatulate, barely emarginate, white, 2–3^{mm} long: capsule linear-oblong, tapering slightly to the apex, 10–13^{mm} long, finely pubescent; the style very short (less than 0.5^{mm} long) but evident; the stigma 2-lobed.

A very distinct species, having its nearest ally in *D. montana* Wats., a plant of more southern range.

Two collections of this were secured in Yellowstone park where it occurs on somewhat shaded, steep, moist slopes: no. 5687 (type), Undine falls, July 6; no. 5922, Yancey's, July 17, 1899.

Lepidium pubicarpum.— Annual, with slender vertical tap root; the stem paniculately branched from near the base, in well developed plants the branches similarly branched, only 9–15^{cm} high including the racemes, obscurely puberulent: leaves small, glabrous or nearly so, linear or somewhat spatulate, acute, the broader ones remotely cut-toothed: beginning to blossom when very small, the fruiting raceme crowded: pedicels short, hardly so long as the capsule: petals wanting, the sepals purplish:

capsule permanently finely pubescent, from broadly oval to orbicular; stigma sessile in the narrow shallow notch: cotyledons incumbent.

Most nearly allied to *L. apetalum* Willd., from which it differs in being lower and more divaricately branched from near the base, while *L. apetalum* has a stem simple at base and branched above. *L. pubicarpum* is not restricted below the flower cluster, since this is very short and the pedicels become gradually divaricate. Its puberulent capsules separate it at once from *L. apetalum*.

Two collections secured: no. 6235, Nez Perces creek, Yellowstone park, July 30; no. 6793, Dwelle's, Mont., August 31, 1899.

Arabis densicaulis.—Biennial or possibly more enduring, the tap root producing several or more often numerous crowded stems from its crown: stems ascending, 3–5^{dm} high (including the raceme), leafy only toward the base, simple or some of the larger ones sparingly branched, glabrous or slightly hirsute near the base: root-leaves crowded-rosulate, oblanceolate, short-petioled, 2–3^{cm} long, finely stellate-pubescent; stem-leaves rather numerous, glabrous, broadly linear or tapering uniformly from a broadish base to an acute apex, auriculate-clasping, the lobes short: flowers small, the petals white or purplish, linear-spatulate, about 5^{mm} long and nearly twice as long as the oblong sepals: the fruiting raceme very long, often two thirds of the whole length; the numerous pods arcuate and widely divaricate or sometimes drooping but not pendulous, 4–5^{cm} long, about 2^{mm} wide, valves obscurely 1-nerved at base; the pedicels about 1^{cm} long: seeds oval, in one row, scarcely winged; the cotyledons oblique, approaching incumbent.

The cotyledons seem to indicate this as a member of the section SISYMBRINA (Syn. Fl. 1: 159), but I am unable to find in any of the known species a close ally. It may be recognized easily by its numerous stems crowded on the crowns, and by the numerous, widely divaricate, arcuate pods of the long, naked racemes.

The type specimens were secured on partly wooded, hard, gravelly, north slopes, near Undine falls, Yellowstone park, July 6, 1899, no. 5680.

Arabis fructicosa.—Similar in size and habit to the preceding, glabrous throughout except for some fine stellate pubescence at base: the stems even more numerous, with more divergent

bases: crown leaves less crowded, some of them sparsely dentate; the stem leaves oblong to ovate, the larger ones dentate: fruiting racemes shorter, the pods broader, scarcely arcuate, divaricate-ascending; the flowers larger as are also the seeds.

No other Arabis is known to me that has the habit of this. A single plant sometimes has fifty or more assurgent stems and forms a hemispherical mat several decimeters in diameter. In this respect the preceding species most nearly approaches it. The two were found in the same locality, but they are at once recognized as different.

The type is no. 5681, Undine falls, July 6, 1899.

Arabis lignipes.— Short-lived perennial, simple-stemmed or more rarely with two or three stems from the summit of the tap root; the woody base of the stem persistent, apparently of as many internodes as the plant is years old, leafless, more or less covered with the old petioles; the internodes variable, usually only 1–3^{cm} long, the whole forming a naked woody foot surmounted by the crown of rosulate leaves at the base of the herbaceous part of the stem; herbaceous stems ultimately 3–5^{dm} high, beginning to blossom when quite low, erect, finely stellate-pubescent below, glabrous upward, becoming smooth throughout in age: the rosulate leaves small and crowded, entire, minutely but densely stellate pubescent, narrowly oblanceolate, tapering to a short petiole, 1–2^{cm} long; the stem leaves numerous, sessile, almost linear, tapering to an acute apex from an auricular sagittate base, slightly longer than the rosulate leaves: raceme crowded in anthesis, open in fruit: pedicels sharply deflexed except in the youngest buds, at first minutely pubescent as are also the sepals, 5–7^{mm} long: petals purplish or sometimes white, narrowly spatulate, 5–6^{mm} long, nearly twice as long as the sepals: pod pendent, straight or curved, smooth, 1-nerved, 6–8^{cm} long, about 2^{mm} broad: seeds in one row, broadly oval, scarcely wing-margined, about 1^{mm} long.

This finds its nearest ally in *A. Holboellii* Hornem., from which its naked woody foot, its invariably simple stems, its smaller entire leaves, and its perennial character separates it.

The following collections of it were secured on dry, sandy or stony bottom lands in Yellowstone park: no. 5503 and 5505, Madison river, June 23, 1900; no. 5583, Glen creek, June 30, 1900.

Arabis pendulocarpa.—Perennial (probably short-lived), a short, simple or branching, woody caudex surmounting a slender tap root : stems 1–3, only one from each crown, simple, ascending, rather weak, about 2^{dm} high, nearly glabrous except at the base which is whitened with simple or branched matted hairs : leaves all entire, crowded on the crowns which are also covered with the remains of those of former years, closely and finely stellate pubescent, narrowly oblong to elliptic, tapering into a short petiole ; the stem-leaves crowded toward the base, linear-oblong, sessile, not auriculate, 5–10^{mm} long, usually longer than those of the crowns : flowers few, small, nearly erect at anthesis but the siliques soon pendent : pedicels 6–8^{mm} long, glabrous or nearly so : petals white or tinged with purple, about 5^{mm} long, distinctly longer than the sparsely hairy sepals : pods 4–6^{cm} long, about 2^{mm} wide ; the seeds narrowly wing-margined.

The key of the *Synoptical Flora* throws this into close proximity to *A. pulchra* Jones, but it is probably more nearly allied to *A. Holboellii* Hornem.

It occurs among the rocks on exposed or partly wooded hilltops. Secured twice, only in Yellowstone park : no. 5504, Madison river, June 23, 1899; no. 5728, Yellowstone river near Junction butte, July 9, 1899.

Arabis elegans.— A tall biennial from a vertical tap root, 6–10^{dm} high : stem simple and strict (rarely a branch or two from the base), a pubescence of branched hairs below, becoming glabrate upward, leafy up to the inflorescence : leaves crowded on the lower part of the stem but not rosulate at the base, mostly entire, more rarely some of them remotely dentate, finely pubescent or the uppermost almost glabrous ; the lower oblanceolate, petioled, passing into the oblong-linear, sessile, auriculate ones of the middle stem ; the upper gradually smaller, linear, sagittate-clasping : raceme either few- or many-flowered ; flowers rather large, from deep purple to almost white, petals almost twice as long as the pubescent sepals ; buds erect but drooping in anthesis ; pedicels ciliate, in fruit ascending, less than 1^{cm} long, bearing divaricate, drooping, or variously curved and twisted pods : pods very slender, 5–8^{cm} long, 1–2^{mm} wide.

This species bears in its habit a marked resemblance to *A. confinis* Wats., but its narrower pods, which are not beaked, the shorter pedicels, and less glaucous appearance will aid in distinguishing it from its eastern ally.

It is of frequent occurrence in the open woods on moist slopes. No. 5601, Mammoth hot springs, June 30; nos. 5676 and 5680, Undine falls, July 6, 1899, the latter being the type number.

Arabis divaricarpa.—In habit resembling the preceding, possibly sometimes perennial, 4–6^{dm} high, glabrous except on the rosulate root-leaves, somewhat glaucous, more or less tinged with purple throughout: root-leaves petioled, slenderly oblanceolate, crowded on the crowns, the pubescence minute and branched; the stem-leaves linear-oblong, sagittate-clasping, 1–4^{cm} long: inflorescence glabrous; the flowers purple to white, smaller than in the preceding: pedicels about 5^{mm} long: pods uniformly divaricate ascending, straight, 3–5^{cm} long, about 3^{mm} broad, most of them conspicuously 1-nerved from base to apex.

Like the preceding species, I can compare it only to *A. confinis*, from which it differs in its broader pod, shorter pedicels, mostly entire leaves which on the stem are rather acutely lobed at the base. The seeds also are quite different; in *A. confinis* small, narrowly oblong; in *A. divaricarpa* rather large and nearly oval.

It was secured in two localities on the open, sandy hillsides overlooking Yellowstone lake, August 1899, nos. 6352 and 6622.

Viola Thorii.—Root mostly simple, semi-fleshy, rather large for the plant: stems several, short, about 15^{mm} high: leaves on petioles 2–3^{cm} long, broadly ovate, truncate at base or abruptly narrowed into the petiole, very coarsely and bluntly dentate, sparsely puberulent below or entirely glabrous, 12–20^{mm} long: peduncles usually surpassing the leaves, very sparsely puberulent, 2–4^{cm} long: sepals linear-lanceolate, glabrous, 4^{mm} long or less: petals about 1^{cm} long, glabrous, yellow, the two upper reddish-brown on the back.

Viola atriplicifolia Greene, which I have not seen, is evidently a close ally, but the species now proposed lacks the cinerous puberulence of that, and has nearly entire leaves in contrast with the hastate or lobed leaves of the other, which also has thickened or flattened petioles.

The type specimens, no. 5816, were secured on the moist, open slopes near the summit of the Thunderer, Yellowstone park, July 13, 1899. I has

also been collected by Dr. Blankinship in Montana and in Yellowstone park, but I am unable to cite his numbers.

Epilobium Wyomingense.—Perennial, spreading by filiform remotely scaly subterranean shoots which end in ovoid winter bulblets with few fleshy scales: stems slender, 2–4^{dm} high, strictly erect, mostly simple, more rarely with slender, erect branches from the axils of the opposite leaves; wholly glabrous below, towards the summit of stems and branches (if any) an obscure puberulence: leaves thin and glabrous, linear, tapering from the middle to both ends, sub-acute, from 3–5^{cm} long (rarely even 8^{cm} long), 2–5^{mm} broad, the uppermost not noticeably reduced, midrib evident, the lateral veins obscure, plane, or the margin barely revolute, opposite except the floral, the few (4–7) pairs nearly equidistant, often shorter than the internodes; those of the branches similar: flowers several, erect, small; the calyx cleft nearly to the base; the petals white, ovate, deeply triangular-notched at apex, 3–4^{mm} long, a little longer than the sepals: capsules linear, 4–7^{cm} long, minutely cinereous-puberulent; the pedicels variable, from much shorter to even exceeding the capsule: stigma oblong or short-clavate, barely notched at apex: seeds numerous, fusiform, smooth, scarcely beaked; the coma white, persistent.

This species is not very closely allied with any of the species known to me, though in a few respects it suggests *E. Oregonense gracillimum* and *E. glaberrimum*. In the more essential characters it seems to be allied to *E. palustre*, from which its longer smooth leaves and smooth stems, and its smooth almost beakless seed separate it.

It occurs in dense patches, on the grassy, boggy banks of spring streamlets. Yellowstone park, no. 5902, Yancey's, July 16; no. 6428, near Snake river, August 12, 1899.

Cryptanthe multicaulis.—Several to many stemmed from the crown of the vertical tap root; the stems rather slender, ciliate-hirsute, erect from a mostly short-decumbent base, sparingly paniculate-branched above, 15–20^{cm} high: leaves rather numerous, broadly linear, 2–3^{cm} long, the unequal, whitish, hispid hairs with pustulate bases: spikes slender, moderately dense even in fruit: sepals setose-hispid, the stouter setae yellowish, the

midrib not evidently thickened, very narrowly lanceolate-acuminate, about 5^{mm} long: nutlets obscurely roughened under a lens, ovate with sub-acute apex, less than 2^{mm} long, the narrow groove forked at base but without conspicuous open areola, similar, usually only three maturing.

This species is allied to *C. Pattersoni* and to *C. ramulosissima*. In habit it is intermediate between them, but in floral and fruit characters it differs essentially from both.

The type number is 6440, from Snake river, Yellowstone park, August 13, 1899.

CRYPTANTHE AFFINIS **flexuosa.**—Evidently allied to *C. affinis*, but a larger plant, 3–5^{dm} high: stems loosely branched from near the base upward, the branches long and flexuous: leaves narrowly oblong, 2–3^{cm} long: fruiting spike long and open: sepals lanceolate-acuminate, densely hispid at base, the tips mostly open and spreading, 6–8^{mm} long: nutlets mottled, smooth and shining, ovate-acute, about 2^{mm} long, the ventral groove nearly closed, forked at the base but without areola.

This may prove worthy of specific rank, but until further material is secured it may best stand as a variety. The species, I think, occurs further toward the west and northwest only.

Secured in Jackson's hole, near Jackson's lake, August 17, 1899.

Mertensia amoena.—Root somewhat woody, more or less branched, surmounted by a branched caudex: branches of the caudex few to several (3–8), crowded, erect, closely covered with dead leaf-bases: stems one or more from each crown, simple, ascending, 1–2^{dm} high, pubescent with short spreading or crisped hairs: crown-leaves oblong-lanceolate, sub-acute, glabrous below, softly hispid-pubescent above and on the margins, 4–7^{cm} long, about one fourth as broad, on slender petioles which are usually longer than the blade: stem leaves rather crowded, broadly linear or narrowly oblanceolate, sessile, 3–6^{cm} long, pubescence similar to that of the root-leaves; inflorescence crowded; calyx-lobes lanceolate, sparsely ciliate-hirsute, about half as long as the tube of the corolla; corolla about 15^{mm} long, the tube scarcely longer than the campanulate limb, the lobes of the limb about half its length, crests inconspicuous; filaments

broad as the anthers, inserted in the throat, the free portion about as long as the anther; the style nearly as long as the corolla.

This is probably a part of the *M. lanceolata* (Pursh) DC. of Gray in Proc. Am. Acad. 10: 53, and of the Syn. Fl. 2: 201, though it is very distinct from what Pursh and De Candolle understood by that species. The original seems to have been that glaucous, glabrous (at most slightly scabrous) plant which we know from the eastern slopes and foothills of the Rocky mountains, and which extends eastward toward the Missouri in the hill regions. That has rather thick fleshy leaves and has fewer stems. I have for years been familiar with it in southern and eastern Wyoming. During the season of 1899 Montana and northwestern Wyoming, where the species now proposed is common, came under my observation. It did not occur to me that anyone could possibly have called it *M. lanceolata*, so different are they in the field. *M. amoena* may be recognized by its cespitose habit, its hirsute (almost cinereous and never glaucous) leaves and stems, and the more crowded inflorescence, which in young plants reminds one of *M. oblongifolia*. It has the habit and leafiness of *M. foliosa*, and is more clearly distinct from *M. lanceolata* than *M. Fendleri* is from that species.

Collected at Monida, Mont., June 15, no. 5413; Glen creek, Yellowstone park, June 29, 1899, no. 5556; at both of which places it was abundant.

Solidago dilatata.—Perennial, from a woody root surmounted by a branched caudex bearing a few surculiferous branches which terminate in a fascicle of leaves: stems single from the crowns, simple, or branched above, rather stout, somewhat striate, glabrous, 4–6^{dm} high: leaves glabrous, conspicuously reticulate-veiny below, minutely scabro-ciliate on the margins; basal leaves oblong-spatulate to elliptic, tapering into a broad margined petiole which is sometimes as long as the blade, either closely or remotely serrate, mostly obtuse at apex, 8–15^{cm} long; the stem leaves numerous, sessile, mostly small (2–3^{cm}): inflorescence nearly glabrous (some ciliate straggling hairs), paniculately corymbose, either compact or quite open, the lower pedunculate branches leafy bracteate: heads numerous, slender-pediceled; the disk about 6^{mm} high; involucral bracts in about three rows, the shorter outer ones very few, the two inner rows sub-equal, minutely ciliate on the margins, linear, most of them obtusish and slightly dilated upwards: rays 8–10, conspicuous; akenes short and lightly pubescent.

This is to be compared with *S. multiradiata scopulorum*, but it is a much larger plant, with larger root-leaves and larger more open inflorescence. In being practically glabrous it also differs from that, and the upwardly dilated bracts especially distinguish it.

It was abundant in loose gravelly soil in the open woods in the southern part of Yellowstone park, no. 6586, August 21, 1899.

Machaeranthera superba.—Probably only biennial, very numerously branched from the crown of the slender tap root: stems decumbent at base and widely spreading, 8–15^{cm} long, each simple below, but paniculately corymbose as to the inflorescence, their purplish hue masked by a minute cinereous puberulence; root-leaves (mostly wanting at flowering time) oblong-lanceolate, with minute spine-tipped teeth, cuspidate-obtuse, tapering into a slender petiole somewhat shorter than the blade, whole length 4–6^{cm}: stem leaves rather numerous, broadly linear to narrowly oblanceolate, entire or remotely denticulate, the teeth and apex cusped as in the root-leaves, minutely and softly subcinereous (scarcely canescent), 3–5^{cm} long, smaller in the inflorescence: heads moderately large, disk about 1^{cm} high, nearly as broad; bracts of the involucre oblong, acute, tips mostly erect, decidedly tinged with purple which is only slightly obscured by the thin puberulence, very rarely a few gland-tipped hairs on the margins: rays 12 (more or fewer), a deep blue (possibly sometimes varying to a purple), length mostly less than 1^{cm}.

Of this species, which was submitted with a number of others, Dr. Greene writes as follows: "A subalpine looking, too showy form of *M. canescens*. But it cannot be referred to *M. subalpina*, however much it looks like it at first glance." Since that was written I have given much study to both of the above species, of which I have typical specimens (the type number of the latter). I am satisfied that the species now proposed is amply distinct from both.

M. canescens as understood (evidently) by Pursh, Nuttall, Gray, and Greene is an essentially erect plant even though branched from the base up, some of its leaves are distinctly serrate or toothed, the bracts are evidently green-tipped, the pubescence is canescent rather than cinereous. *M. superba* is more nearly allied to *M. subalpina*. This it resembles in the relatively few (as compared with *M. canescens*) showy heads and in the character of the pubescence. It is distinguished from it by the almost entire absence of viscid

or glandular hairs, and from both by its less erect habit and by its broad, colored involucral bracts.

It occurred in the greatest abundance in one locality only, an open, sandy hillside near Yellowstone lake. The depressed, mat-like plants, with their relatively large, showy heads, were singularly attractive and invited the closest attention. The type number is 6337, from the Thumb, August 6, 1899.

Erigeron Yellowstonensis.— Biennial, or probably many of the plants more enduring, with a strong vertical tap root: generally only one stem from the enlarged crown (more rarely 2–5), simple, stout, striate, erect, paniculately branched as to the inflorescence, 3–6^{dm} high, purplish, glabrate, the whitish hairs very straggling, obscurely granular (scarcely glutinous): leaves numerous, pubescence nearly wanting, similar to that of the stem; crown leaves oblanceolate, petioles 3–6^{cm} long; lower stem leaves similar but with short winged petioles; upper leaves sessile, narrowly lanceolate, not much reduced, the short branches of the panicle from their axils; bracts small, linear: heads numerous, on rather slender peduncles; involucral bracts dark green, in two rows, subequal, very narrow, acuminate, shorter than the 1^{cm} high disk: flowers very numerous; rays filiform, purplish, only moderately numerous, largely concealed by copious pappus: akenes linear, appearing glabrous but sparsely pubescent under the microscope, less than 2^{mm} long; the soft, dirty-white pappus nearly three times as long.

The *E. Droebachensis* Mueller (*E. acris Droebachensis* (Muel.) Blytt.) of Europe is unknown to me, but I cannot read the description of that into the plant now proposed as a species. Neither does it seem probable that any of the other usually accepted synonyms of *E. Droebachensis* represent this plant, for they also refer to European or arctic forms, except the *E. glabratus* of Hooker's *Flora*. The latter seems to have spatulate root-leaves, the cauline ones almost linear; a racemiform inflorescence, with very long lower peduncles, making an approach to a corymb; the pappus of a more yellowish hue.

This plant was found in abundance near Yellowstone lake, in the open pine woods, in loose sandy soil: nos. 6348 and 6615, the Thumb, August 1899.

ERIGERON MULTIFIDUS **incertus.**— Caudex densely cespitose; its branches comparatively long and woody, roughened with the

old leaf-bases: stems usually two or more from each crown, rather slender, curved ascending or erect, 12–18^{cm} long, sparsely ciliate and obscurely granulo-puberulent, monocephalous: leaves crowded on the crowns, green and appearing glabrate but ciliate on the petioles and often on the blades, obscurely granulo-pubescent, simply three-parted, or more often each segment again three-parted; ultimate segments linear-oblong, 4–6^{mm} long; petioles slender, 2–3^{cm} long; stem leaves few (2–4), bract-like, mostly linear, entire, the lower occasionally trifid: heads 8–12^{mm} high, rays wanting (apparently sometimes a few filiform ones); disk flowers very numerous; involucre ciliate-pubescent and granulo-glandular under the longer hairs, bracts linear-acuminate, equaling the disk: mature akenes flattened, narrowly obovate, finely pubescent, about 2^{mm} long; the soft pappus about twice as long as the akene.

This variety holds about the same relation to *E. multifidus* Rydb. (Fl. Mont. & Y. N. P. 402) as the variety *glabratus* does to the same species. The two varieties resemble each other in habit and leaf outline. They are both glabrous in appearance, but only the one is wholly glabrous and the other is eradiate. The variety *incertus* differs from *E. multifidus discoideus* in its larger size, in being more glabrate, and in its cespitose caudex.

Nos. 5538 and 6066 from Yellowstone park belong here, as does also no. 2343 from Dome lake in the Big Horn mountains, 1896. It occurs on dry stony hills and is fairly abundant.

ARNICA CHAMISSONIS **longinodosa.**—Stems single from horizontal rootstocks from which spring numerous, thick, fibrous roots, erect, 4–8^{dm} high, the internodes long, usually 10–15^{cm}, much exceeding the leaves or rarely only equaling them: pubescence of two kinds, a short, dense, glandular puberulence (especially on the peduncle), and some scattering white crisped hairs (especially on the involucre): leaves 3–5 pairs, denticulate; the lowest pair oblong-oblanceolate, 6–10^{cm} long, on slender petioles often as long, disappearing early in the season or, at least, rarely collected; the next lowest mostly obovate or narrower, tapering into a short margined petiole, variable in size, either shorter or longer than the lowest pair; the upper pairs sessile by a broad base, very variable in size and shape, from

ovate to oblong, 5–15^{cm} long: heads 1–3, mostly single and then long-peduncled; if more, then from the axils of the uppermost leaves which are often much reduced, occasionally only one of the leaves and lateral peduncles developing; lateral peduncles equaling or even exceeding the terminal, 1^{dm} (more or less) in length: heads large (if more than one somewhat reduced), disk 15–20^{mm} high, 20–30^{mm} broad; rays about twelve, 20–30^{mm} long, 6–8^{mm} broad; involucral bracts 14–20, lanceolate, acute, shorter than the disk: akenes striate, nearly linear, but tapering to the base, obscurely short-hispid on the angles, about 5^{mm} long, equaling the sordid, sub-plumose pappus.

I have described this in detail, for I believe that it will ultimately be shown that this is a good species rather than a variety. The *A. Chamissonis* Less., from Unalashka, seems to be a much more pubescent plant, with narrower leaves and more pubescent akenes, the internodes, as compared with the leaves, relatively shorter.

The following numbers represent some of the collections of this species in Wyoming: 1702, 1785, 3571, and 6379, the last from Yellowstone park, August 1899. M. E. Jones no. 5883, from Utah, is this species.

Arnica Columbiana.—Perennial, 4–8^{dm} high: stems rather stout, erect, striate, simple below, paniculately corymbose above, with some lanate white pubescence: root-leaves not known; stem leaves several (six or more pairs not counting the rameal), the lower apparently petioled, the middle and upper ample, sessile, clasping, entire, rather conspicuously nerved, oblong, sub-acute, finely pubescent below, obscurely so above, 8–14^{cm} long, 3–5^{cm} broad; rameal leaves and bracts ovate, the smaller ones acuminate: inflorescence an ample panicled cymose corymb of 15–30 or more rather unequal heads: involucral bracts 20 (more or less), oblong, sub-acute, shorter than the disk: rays 12 or less, 10–14^{mm} long, 3–4^{mm} broad: akenes small, 5-nerved, linear-subcylindric, tapering to a slender base, only about 3^{mm} long, shorter than the sordid pappus.

Of this unusually distinct species I have seen but two specimens, both of which are in the herbarium of the Montana State College.

The type is Mrs. J. J. Kennedy's no. 24, Columbia falls, Mont., 1894 Mr. R. S. Williams' no. 1049, from the same locality, June 14, 1894, is the

same as to the larger specimen (on the sheet before me). Both were distributed as *A. amplexicaulis* Nutt., to which they bear but little resemblance. Mrs. Kennedy's specimens are included by Dr. Rydberg in his *A. amplexifolia* (Nutt.) of his *Flora of Montana.*

Arnica ocreata.— From slender horizontal rootstocks: stems slender, 3–4^{dm} high, erect, very leafy, nearly glabrous, more or less finely granular-glandular, occasionally some straggling woolly hairs: leaves 6–10 pairs, ascending or erect, from broadly to narrowly lanceolate, entire, sub-acute, gradually smaller upward, and becoming bract-like, all but the uppermost much exceeding the short internodes (even overlapping two or three of the internodes), the lowest petioled, the uppermost sessile: petioles slender, dilated at the base and connate, the pair forming an ocrea or sheath which in the lowest leaves is 2–3^{cm} long, the sheath and petioles gradually shorter upward to about the middle of the stem where both become wholly absent: heads one to several; if three, corymbose, the two from the axils of opposite bracts; if more than three, mostly somewhat racemose from the axils of alternate bracts; terminal head largest, disk 10–12^{mm} high, exceeding the oblong, obtusish bracts, about 15^{mm} broad; rays about 1^{cm} long; lateral heads somewhat reduced: pedicels variable, rather slender, very lightly woolly-pubescent: akenes nearly glabrous, lightly striate, somewhat flattened, narrow, tapering to the base, nearly equaling the soft pappus.

This is in part, so far as specimens in the collections go, *A. foliosa.* It is not the *A. foliosa* of Nuttall, which is probably a rarer plant, though collections of that are not infrequent. That, as may be seen by the original description and as may be be gathered from Hooker's *Flora* and from Torrey and Gray's *Flora N. A.* (where it was compared with *A. montana* and *A. Chamissonis*) is a very different plant, and nearly allied to *A. Chamissonis. A. foliosa* has the stout, strict habit of that, is tomentose pubescent, somewhat equally leafy throughout, the leaves callous-denticulate, evidently nerved (about five), the heads congested-corymbose and the akenes hirsute. *A. ocreata* may be recognized at once by the characteristic disposition of its entire, rather narrowly lanceolate leaves. Owing to their diminution in size upward and the comparatively long petioles of the lower (some of them disappearing early) the strict leaves have the appearance of being crowded near the middle, while the base and summit of the stem are semi-nude.

This species occurs on wet bottom lands in the edges of copses of undershrub. Typical collections of it are nos. 766 and 1195, Wind river, Wyoming, Aug. 1894, by *Nelson;* no. 5224, Shoshone lake, Aug. 1897, by *Rydberg & Bessey;* no. 6403, Snake river, Aug. 1899, by *Nelson & Nelson;* Silverton, Colo., July 1898, by *C. S. Crandall* (distributed as *A. longifolia*).

Arnica polycephala.—Nearly allied to and much resembling *A. longifolia* Eaton, but larger than that species, forming larger and denser clumps, the stems very numerous: leaves lanceolate, less acuminate than in *A. longifolia*, glabrous or obscurely granulo-glutinous: heads moderately large, very numerous (20–50) on each stem which is paniculately branched above.

This might possibly be considered only a variety, but it is at once distinguished from its ally by the absence of the puberulence of that species, by the less acuminate leaves, and the several times more numerous heads.

It was found growing in great masses among the rocks of the slides, of the steep cliffs overlooking Snake river near the southern boundary of Yellowstone park. The type is no. 6422, Aug. 12, 1899.

Arnica exigua.—Low, 1–2^{dm} high, sub-cinereous hirsute-pubescent throughout, with an obscure granular glutinosity beneath: stem erect, corymbosely paniculate-branched from the base upward; the branches ascending, often a pair from each node, each bearing one or two heads: leaves mostly lanceolate, acute; the two or three pairs on the main stem 5–8^{cm} long, all sessile; those on the branches similar but smaller: heads of medium size, involucral bracts oblong, sub-acute, nearly equaling the disk which is 10–15^{mm} high; rays in well developed heads twelve or more; akenes very narrow and tapering to the base, nearly glabrous.

This is a species of unusual habit. It has the appearance of a plant which has put out new shoots after being browsed off and stunted by some animal. An examination, both in the field and of the specimens collected, shows that this is not the case, and that this dwarfed plant is perfectly normal. It is an ally of *A. foliosa* Nutt., of which I at first suspected it being a deformed state. The habitat of the two is different. *A. foliosa* is found on the fertile soils of wet bottom lands.

The specimens of *A. exigua* were secured on the higher, dry sandy bluffs and ridges overlooking Yellowstone lake. The type is no. 6940, Aug. 24, 1899.

Arnica caespitosa.— Low ($1–2^{dm}$), matted, sometimes forming beds several decimeters across, with moderately large woody horizontal rootstocks from which spring numerous thick fibrous roots, the whole forming a dense turf: the numerous stems erect, sparsely short-lanate as is also the base of the involucre: leaves nearly glabrous or sparsely ciliate-woolly, three or four pairs on the stems and some fascicled ones on the sterile crowns; crown leaves mostly oblanceolate, petioled, $4–7^{cm}$ long (including the petiole); basal stem leaves very small (often wanting), obovate as also the next larger pair; upper leaves lanceolate: heads one to five, large for the size of the plant, mostly three (a terminal one and a pair from the uppermost axils); pedicels moderately stout, $2–5^{cm}$ long: involucres turbinate; bracts linear-oblong, sub-acute, almost equaling the disk; rays 8–10, ascending, rather broad: akenes linear, white-pubescent, about 5^{mm} long, equaling the white, glistening pappus.

An excellent species of nearly alpine stations; occurring in patches on nearly naked, rocky slopes. It may be recognized by its cespitose habit and dense root-system, its turbinate head (the rays are ascending also), and the white-pubescent akenes.

Collections of it are no. 5785, Druid peak, Yellowstone park, July 12; no. 6717, Teton mountains, Aug. 16, 1899.

LARAMIE, WYO.

BRIEFER ARTICLES.

PHOTOGRAPHY IN BOTANY AND IN HORTICULTURE.

(WITH TWO FIGURES)

ALMOST every working scientist knows something about photography, and probably no one will deny that a camera is one of the indispensable equipments in every well-regulated botanical or horticultural laboratory. Yet a casual acquaintance among various horticulturists and botanists, and the repeated publication of unnecessarily inadequate (not to say atrociously bad) photographs, lead us to believe that the use of the camera in horticultural and botanical work will bear some discussion. We are convinced that the value of the camera as a piece of scientific apparatus is not generally appreciated. We believe that the camera is not used as often as it ought to be, and we believe yet more strongly that the photographic methods with which many science workers content themselves are not really creditable. We believe that as a help in daily work, the camera ranks next to the microscope for the botanist, and far above the microscope for the horticulturist. Yet while every laboratory has a row of books on microtechnique, and while every botanist and most horticulturists work hard to perfect themselves in microscopical methods, a book on photography is a rarity, and men are satisfied to blunder along with almost any sort of a camera, and with plates and developers of which they know practically nothing. Some even are willing to "press the button" and let some company in another state "do the rest."

In the matter of photographing plants, fruits, flowers, and similar objects,[1] we may perhaps offer a few observations as the result of experiments covering several years.

The particular piece of apparatus required for this sort of work is some support which will hold the camera approximately in a vertical position, and will provide a transparent horizontal shelf some distance from the floor. The objects are laid on the latter and the camera is focused down upon them.

[1] "Photographing flowers and trees," *The Photo-Miniature*, No. 13, April 1900.

Any sort of construction which provides for the vertical camera and the horizontal shelf will answer, and several different forms are actually in use. *Fig. 1* is sketched from a photograph of the apparatus in use at the Vermont Experiment Station. *Fig. 2* shows a more elaborate form, designed by Mr. McFarland and used at the Mt. Pleasant Printery. The construction will be obvious in either case, and may be modified to suit individual needs. Lightness, rigidity, and portability are the chief requirements in an apparatus for field use; while in the studio the permissible increase of weight makes a somewhat more convenient construction available. *Fig. 2* is especially a studio camera-stand, adaptable for both vertical and horizontal work, making lantern slides, enlargements, etc.

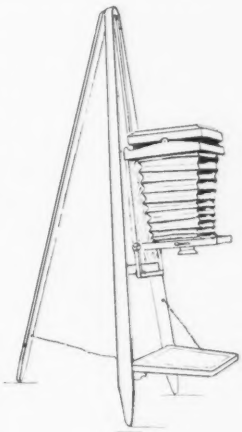


FIG. 1.

The advantages of such an apparatus are: (1) It does away with nearly all trouble in arranging the subject. Simply lay a plant, some flowers, specimens of fruit, or other objects on the glass shelf, and they stay where they are put. In the case of fruits, which will not always lie where wanted, one should have at hand a supply of rubber hose-washers, *i. e.*, rubber rings 3–4^{cm} in diameter. Set the fruit into the ring, and it may be moved anywhere and put in almost any position. (2) It allows one to arrange any background desired. Sheets of cardboard in white, black, and neutral tints may be successively tried behind the subject and the best one chosen. (3) It does away with shadows which are almost inevitable and frequently disastrous in any other method of plant photography. (4) It facilitates considerably the work of making exact size photographs of objects. For all sorts of floral and fruit photography it is much the best way to have all photographs (with a few necessary exceptions) made exact size. This is especially desirable when one begins to have a collection of negatives numbering into the thousands.

For comfortable plant, flower, vegetable, or fruit photography in full natural size, a camera with considerable bellows extension is essential. To obtain a natural size image the lens must be equidistant between the object and the ground glass of the camera at twice its focal length. Thus, if for a plate of $6\frac{1}{2} \times 8\frac{1}{2}$ inches a lens of $7\frac{1}{2}$ inches

focal length be used, sufficient bellows must be at hand to permit the ground glass to be fixed at 15 inches from the objective. The modern "long-focus" cameras provide very fully for this need and others which will appear upon trial. The best work will be possible if a lens is chosen of rather short focal length, one technically known as a "wide-angle" lens. Not only is the range of the camera thus increased, but the sharp focus over a considerable depth which is absolutely requisite in morphological work is far more easily obtained.

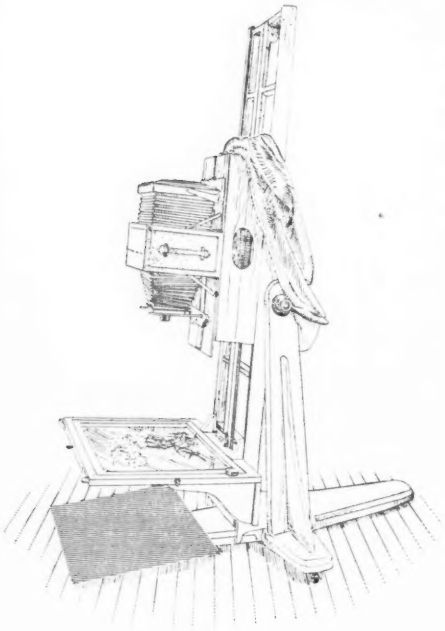


FIG. 2.

In focusing, it will be found a decided advantage to select a spot in the object or composition upon the glass shelf a little above its vertical center, and there to affix temporarily a white card or paper with fine lines. An ordinary visiting card is excellent. When this is focused upon, and the lens then "stopped down," the whole object will be sufficiently sharp. We urge extreme care and cleanliness in all photographic operations. In working full size, dust is a great enemy; every grain is willing to be photographed.

A skylight is most undesirable for vertical photography, because of the reflections upon the glass platform. Indeed, the worker will find it almost essential to guard against reflections from the skylight, the ceiling of a light room, and particularly from the polished camera front and lens, by preparing a wire frame or hood, covered with black velvet or the like, and extending about the camera so as to cut off the immediate top light.—F. A. WAUGH and J. HORACE MCFARLAND.

CURRENT LITERATURE.

MINOR NOTICES.

T. Ito and J. Matsumura[1] have begun the publication of a catalogue of the flora of the Lûtchû Islands, the archipelago between Japan and Formosa. The present work, written in English, is intended to be a preliminary contribution to the knowledge of the flora of these islands, containing merely the bibliography, synonymy, and local and general distribution of the plants, with occasional descriptions and critical notes. The Leguminosae, including about 125 species, are specially worked out by Professor Matsumura, a number of new species being described. The flora is one of exceptional interest, and such a compact and complete presentation of it will be welcome to botanists. — J. M. C.

O. Warburg has begun the publication of the flora of the monsoon regions of southern and eastern Asia, selecting as his title *Monsunia*.[2] The typography is sumptuous, and the plates are of the highest quality. A brief itinerary shows a most extensive personal experience throughout the vast region indicated by the title. The Fungi are by P. Hennings, *Phaeolimacium* (Agaricaceæ), *Nymanomyces* (Hysteriaceæ), *Phaeorhytisma* (Phacidiaceæ), *Cerocorticium* and *Discocyphella* (both Thelephoraceæ), *Pseudotrype* (Hypocreaceæ), *Pseudotthia* (Melanommaceæ), *Schizacrospermum* (Acrospermaceæ), *Janseella* (Stictaceæ), and *Phaeomacropus* (Pezizaceæ) being new genera from Java. The Algæ by F. Heydrich, and the Hepaticae by V. Schiffner have been for the most part already published elsewhere. The Musci are by V. F. Brotherus (*Warburgiella* being a new genus), and the Filicineæ by H. Christ, the latter group naturally having a very extensive representation. The other pteridophyte groups are presented by Warburg, and abound in new species and critical notes. The genus Selaginella is especially considered, being represented by 184 species, forty-seven of which are ascribed to the author, and its geographical distribution is discussed. The gymnosperms, which close the volume, are also by Warburg, and this part is full of interest, containing as it does descriptions, fine illustrations, and distribution of many of the little known and more critical forms.— J. M. C.

[1] Tentamen Florae Lutchuensis. Sectio I. Plantae Dicotyledoneæ Polypetalae. Separate from Jour. Sci. Coll. Imperial Univ., Tokyo, **12**: 263–541. 1899.

[2] Monsunia, Beiträge zur Kenntniss der Vegetation des süd- und ostasiatischen Monsungebietes, Vol. I, pp. 207. *pls. 1–11*. 1900. Leipzig: Wilhelm Englemann. *M* 40.

NOTES FOR STUDENTS.

THE "PROTEID VACUOLES" of gymnosperms have recently been reinvestigated by Arnoldi.[3] These structures were described by Hofmeister nearly fifty years ago as "Keimbläschen" (germinal vesicles) and he makes the statement that the archegonium of the vascular cryptogams differs from that of the gymnosperms in having only one nucleus (Keimbläschen) while that of the gymnosperms has many. Schacht, who wrote at about the same time, regarded the structures as cell-sap vacuoles, while Strasburger, at a considerably later period, regarded them as proteid vacuoles.

Goroschankin (1883), who made some study of their development, found that they differ from the sap vacuoles, and make their appearance before the cutting off of the ventral canal cell, disappearing during the formation of the embryo.

The present writer, with the aid of modern technique, has attacked the old problem of the origin and development of the bodies and finds that they are genuine nuclei. The nuclei of the cells of the tapetal layer immediately surrounding the oosphere put out amoeboid processes which penetrate the cell wall, and soon the whole nucleus passes through the opening and into the cytoplasm of the egg, where they become more or less modified so that while they bear a striking resemblance to nuclei they could not be positively identified as such except by tracing them back to their origin. Nuclei were also observed to pass from the next layer into the cells of the tapetal layer. The paper is only a preliminary one, but the stages figured are strong evidence in favor of the author's view. These bodies serve only for the nutrition of the embryo and take no part morphologically in its development.—CHAS. J. CHAMBERLAIN.

DUNCAN S. JOHNSON has been investigating *Saururus cernuus*[4] in reference to the claim made by Engler and others that it is a primitive dicotyledonous type. He finds in the developing ovule a one-celled archesporium; a "tapetal" cell is cut off, which gives rise to but few cells; the megaspore mother cell organizes a row of three, the lowest of which becomes the functioning megaspore; the ante-fertilization development of the sac structures is as usual; the antipodal cells are evanescent. After the ante-fertilization stage is reached the sac grows rapidly, especially in length, and finally broadens below, remaining narrow at the top, thus appearing as a long-necked flask, with the primary endosperm nucleus lying at the base of the neck. At the first division of this nucleus one daughter nucleus remains in

[3] ARNOLDI, W.: Beiträge zur Morphologie der Gymnospermen. IV. Was sind die "Keimbläschen" oder "Hofmeister's Körperchen" in der Eizelle der Abietineen? Flora **87**: 194–204. *pl. 6, 7.* 1900.

[4] On the development of *Saururus cernuus* L. Bull. Torr. Bot. Club **27**: 365–372. *pl. 23.* 1900.

the neck, the other moves down into the body of the flask, and a wall is formed across the base of the neck, giving rise to two endosperm chambers. The upper endosperm nucleus divides and forms a compact tissue in the upper chamber; while the other enlarges but never divides, the lower and larger endosperm chamber apparently being related to the adjacent perisperm as an absorbing organ. In the upper chamber the embryo is organized, and the endosperm about it encroaches upon all the nucellar tissue adjacent to it.

The germination of the seed is also very peculiar, the endosperm emerging first, and retaining hold of the cotyledons and supplying nutrition after the cotyledon tips have carried the old seed well up into the air. The author concludes that there is no evidence that Saururus is more primitive in character than many other dicotyledons.— J. M. C.

FR. SCHAIBLE has devised an apparatus for research on the effect of diminished air pressure on plant growth,[5] in which the plants can be cultivated for a considerable time without being in a stagnant atmosphere and without being subjected to repeated evacuation of the culture chamber. The essential feature is the use of a tubulated bell jar to which air is admitted through a capillary tube, a water pump in continuous operation serving to exhaust the chamber more rapidly than the air can enter through the capillary passage.

He finds, in agreement with Wieler and Jaccard, that ordinary growth is accelerated, especially that of the leaves, while germination is retarded and is of lower percentage. Investigation of the question whether these results are due to diminished pressure, as such, or to diminished partial pressure of oxygen, leads Schaible to conclude that the retardation of germination is due to the diminished O pressure. The acceleration of growth, however, is not due to this cause (which really tends to retard growth slightly), nor to lessened CO_2 pressure, nor to the altered light, heat, or moisture. The only possible explanation seems to be that the plants absorb water more rapidly under the lower pressure (isolated cylinders of live pith do so), and consequently the cells reach their definitive size more quickly, thus attaining earlier the stage of division. The copious guttation observed both by Döbereiner and Schaible also accords with this explanation.—C. R. B.

ITEMS OF TAXONOMIC INTEREST are as follows: A. ENGLER (Bot. Jahrb, **28**: 385–510. 1900) has completed his account of the flora of the Lake Nyassa region, describing numerous new species. *Neogoetzea* Pax (Euphorbiaceæ), *Linnaeopsis* Engler (Gesneriaceæ), *Megalopus* K. Schumann (Rubiaceæ), and *Ageratina* C. Hoffmann (Compositæ), are the new genera.— HENRY DEANE and J. H. MAIDEN are publishing in Proc. Linn. Soc. of South Wales a series

[5] Fünfstuck's Beitr. z. wiss. Bot. **4**: 93–148. 1900. See also Bot. Centralbl. **82**: 52. 1900.

of papers entitled "Observations on the eucalypts of New South Wales." The last one issued (Proc. Linn. Soc. **4**: 612–630. *pls. 48–50.* 1900) is the sixth, and includes descriptions of three new species.— E. P. BICKNELL (Bull. Torr. Bot. Club **27**: 373–387. 1900), in continuing his "Studies in Sisyrinchium," has revived Salisbury's genus *Hydastylus* to receive the yellow-flowered *S. Californicum*, and has associated with it 11 other species, 9 of which are described as new.— K. M. WIEGAND (*ibid.* 388–391) has described two new species of *Saxifraga* and one of *Primula* from the northwest.— C. V. PIPER (*ibid.* 392–401), in continuing his "New and noteworthy northwestern plants," describes new species of *Amelanchier, Potentilla, Saxifraga* (3), *Townsendia, Erigeron, Castilleia* (2), and *Salix* (2).— KATHARINE BRANDEGEE (Zoe **5**: 31–35. 1900), in her third paper entitled "Notes on Cacteæ," describes two new species of Mamillaria, besides giving critical notes on several other forms.— C. WARNSTORF (Hedwigia **39**: 100. 1900) has described four new Sphagna from Virginia and North Carolina collected by T. H. Kearney.—J. M. C.

MR. HAROLD WAGER has published the results of his study of the fertilization of *Peronspora parasitica*,[6] his conclusions being as follows: the protoplasm of the oogonium differentiates as usual into vacuolate ooplasm and granular periplasm; a receptive papilla is formed on the oogonium in contact with the antheridium and is penetrated by the antheridial tube; the nuclei of the oogonium and antheridium undergo mitosis before fertilization; soon after the delimitation of the oosphere the central body appears, which seems to play some part in bringing the sexual nuclei together; a single nucleus from the periplasm travels towards the central body, coming in close contact with it, and towards it the antheridial tube advances and discharges a single nucleus; fusion occurs while the nuclei are in the resting stage and not until the oospore is nearly ripe; the central body disappears before fusion; the ripe oospore is uninucleate; no difference is observable between the sexual nucleus and those that remain in the periplasm, all probably being potentially sexual; three types of fertilization and oospore-formation in the Peronosporeæ may be distinguished, as follows: (1) uninucleate oosphere, binuclear fusion, and uninucleate oospore (*P. parasitica*); (2) uninucleate oosphere, binuclear fusion, and multinucleate oospore (*C. candidus, C. Portulacae*, and *P. Ficariae*); (3) multinucleate oosphere, multinuclear fusion in pairs, and multinucleate oospore (*C. Bliti*).— J. M. C.

A PRELIMINARY paper by Lidforss[7] records some interesting experiments upon the chemotropism of the pollen tube. *Narcissus Tazetta* furnished material for most of the work.

If the pollen be placed in a 5–15 per cent. sugar-gelatin solution and a piece of stigma be added, the pollen tubes soon turn toward the stigma, as is already

[6] Annals of Botany **14**: 263–279. *pl. 16.* 1900.

[7] LIDFORSS, B.: Ueber den Chemotropismus der Pollenschläuche. (Vorläufige Mittheilung.) Ber. d. deutsch. bot. Gesell. **17**: 236–242. 1898.

known. Lidforss finds that organic acids, formic, acetic, succinic, lactic, tartaric, malic, etc., as well as amides, glucosides, and tannins, do not produce any undoubted effect upon the direction of growth of the tubes. Diastase, however, produces an almost immediate effect, and experiments show that it is the proteid constituent of the diastase which attracts the pollen tube. Further experiments show that carbohydrates and proteids are the substances which influence the direction of growth and indicate that the movement of the pollen tubes is for the purpose of securing nutrition.

The pollen of most Liliaceæ is more sensitive to mineral salts than Narcissus pollen, the same diastase preparation which attracts Narcissus pollen quickly killing the pollen of Fritillaria, but if the salts be dialyzed out the proteid exerts a strong influence upon Fritillaria pollen.—CHAS. J. CHAMBERLAIN.

IN AN ADDRESS before the Niederrheinische Gesellschaft für Natur und Heilkunde zu Bonn,[8] Dr. F. Noll[9] makes a suggestion which is likely to prove fruitful, because it not only groups together some previously isolated facts, but seems likely to be the starting point of further investigations. He has been led to believe that the *form* of the plant body itself is a source of both orienting and formative stimuli. As evidence of this he appeals to the fact that in regions of curvature the concave side of roots remains entirely free of lateral rootlets, which are limited to the convex side; or, if they appear at all upon the neutral flanks, they bend more or less sharply toward the convex side. These phenomena have been observed in all the plants studied, including representatives of all the great groups which develop roots.

With these facts Noll correlates Wiesner's "exotrophy," a widespread phenomenon, whereby the growth of external members or their external flanks is conspicuously promoted as compared with that of corresponding members situated toward the interior. Vöchting's "rectipetality," Pfeffer's "autotropism," and the phenomena of replacement, regeneration, and polarity have a new light cast upon them by Noll's suggestion. Many old fields also need exploring from this new point of departure.—C. R. B.

THE DISCOVERY by A. C. Hill that the hydrolysis of maltose by maltase is a reversible process and that this enzyme is also capable of forming maltose from glucose[10] seems to be supported by the results of M. Cremer's investigations.[11] He finds that the glycogen-free expressed extract of yeast is capable of producing glycogen in a 30 per cent. solution of fructose, which is

[8] Sep. Abdr. aus d. Sitzungsber. d. Niederrhein.. Gesells. 1900; Sitzung von Jan. 15. 1900. pp. 6.

[9] Noll's extended researches are announced to be published in Thiel's Landwirthschaftliche Jahrbücher early in this year.

[10] Trans. Chemical Soc. **1898**: 634–658.

[11] Berichte d. deutsch. chem. Gesells. **1899**: 2062–2064.

a still more complex process than the production of maltose from glucose. Meyer suggests [12] that similar relations may exist among other polysaccharides which are hydrolyzed by enzymes. Holding that the enzyme which digests starch has its origin in the plastids,[13] he now thinks it probable that this enzyme acts like maltase. When a concentrated solution of sugar enters the stroma from the cytoplasm, amylose is formed, which on reaching a certain concentration crystallizes out in the form of a starch grain; while if sugar is wanting in the cell a relatively active inversion of amylose occurs, and a rapid solution of the starch grains. The suggestion is interesting and deserves careful testing.—C. R. B.

MR. W. H. LANG has published the second number [14] of his series entitled "Studies in the development and morphology of cycadean sporangia," dealing with the ovule of *Stangeria paradoxa*. His results are as follows: two ovules are developed on each sporophyll; the archesporium consists of a mass of cells, one of which is selected, enlarges very much, and forms a row of three, the lowest cell of which organizes the megaspore; at the time of pollination the sac is full of endosperm (but without archegonia), the pollen chamber is fully developed within the beak-like process of the nucellus, but the breaking down of nucellar tissue between the pollen chamber and the embryo-sac has not begun; as in Cycas and Zamia, the sperms are large, spirally twisted, and multiciliate, with the blepharoplast band evident; disorganization of endosperm tissue between the pollen-chamber and the embryo-sac gives free access to the latter, and the sperms are discharged into the archegonial chamber of the nucellus, reaching the neck by swimming.— J. M. C.

HUGO DE VRIES has been experimenting in hybridizing the races of maize,[15] producing the well-known phenomenon of xenia. Associating his results with those of Nawaschin and Guignard, who have announced the discovery of double fertilization in the embryo-sac of certain liliaceous plants, he has reached the conclusion that the hybridization of the embryo is always accompanied by the hybridization of the endosperm, and that this phenomenon can only be explained by double fertilization. He found that every grain whose endosperm showed the characters of the pollinating parent had a hybrid embryo; and that every grain whose endosperm showed the characters of the embryo-sac parent had an embryo of pure race, and was therefore self-fertilized. In a few words he puts it that double fertilization is corroborated by double hybridization.— J. M. C.

[12] Bot. Zeit. **57**[2]: 313. 1899. [13] Untersuch. über Starkekörner 169.

[14] Annals of Botany **14**: 281–306. *pls. 17–18.* 1900.

[15] Sur la fécondation hybride de l'endosperme chez le maïs. Rev. gén. de Botanique **12**: 129–137. *pl. 15.* 1900.

GEORGE MASSEE, in discussing the origin of the Basidiomycetes,[16] presents the following summary: (1) in the conidial condition certain ascigerous fungi bear their spores on structures morphologically indistinguishable from the basidia of the Protobasidiomycetes; (2) some members of the same form genera as those described in (1), as *Stilbum vulgare* Tode, have lost the ascigerous condition from their life cycle, and are accepted as true Protobasidiomycetes; hence we are justified in concluding that the Protobasidiomycetes as a group originated from ancestors that represented the conidial condition of ascigerous fungi; (3) there is no evidence in favor of the suggestion that the Autobasidiomycetes are descended from the Protobasidiomycetes; on the other hand, the evidence in favor of the Autobasidiomycetes having been derived by gradual modification of the spore-bearing organs, or basidia of conidial forms of certain ascigerous fungi, is not lacking.— J. M. C.

J. W. TOUMEY has published the results of his study of "crown-gall" as Bulletin 33 from the Arizona Agricultural Experiment Station, under the title "An inquiry into the cause and nature of crown-gall." The name is applied to a disease which appears as fleshy outgrowths on the roots of deciduous fruit trees, usually at the crown. The author concludes that the cause is a specific organism, one of the Myxomycetes, parasitism among which has been thought to be confined to a single species (*Plasmodiophora brassicae*, which causes "club root" in cabbage and allied plants). The plasmodium and its effect upon the host cells are fully described, as well as the sporangia. The study of the organism is made the occasion of the establishment of a new genus, *Dendrophagus*.— J. M. C.

NOW THAT TRIPLE FUSION has been discovered in connection with the formation of the primary endosperm nucleus, illustrations are rapidly multiplying. First announced by Nawachsin for *Lilium Martagon*, it was confirmed for the same species by Guignard and Miss Sargant, the former adding other species of Lilium and also Fritillaria and Tulipa. Now Miss Ethel N. Thomas finds vermiform nuclei wrapped about the polar nucleus in *Caltha palustris*;[17] while Nawaschin has described and figured[18] triple fusion in the embryo-sacs of *Helianthus annuus*, *Rudbeckia speciosa*, and *Phaius Blumei* (an orchid).— J. M. C.

WARNSTORF gives[19] a description of the anatomical characters of a number of the species of Sphagnum which have not previously been examined with the thoroughness and minuteness which modern taxonomy demands in this group. The characters are drawn from types, and the examination of

[16] Jour. Linn. Soc. **34**: 438–448. *pls. 15–16.* 1900.

[17] Annals of Botany **14**: 318–319. 1900.

[18] Ber. d. Deutsch. bot. Gessell. **18**: 224–230. *pl. 9.* 1900.

[19] Bot. Cent. **82**: 7 sq. 1900.

these has led to the reduction of many of the recently proposed species, particularly those of C. Müller, whose later work was so prolific of "new" species. Some of the critical remarks touch American and Antillean species. —C. R. B.

VON DERSCHAU has studied carefully the process of wall thickening in the formation of the teeth of mosses.[20] He finds that preceding the true thickening process, the activity of the cytoplasm consists only of its preliminary accumulation on the membrane to be thickened. In this the nucleus exerts no clearly recognizable control, but does do so in the thickening process itself. This consists of the apposition of materials early produced in the cytoplasm, of which cellulose is the primary one, the other substances being such as promote hygroscopicity and resistance to decay.—C. R. B

DR. GEORG GOETZ has restudied the development of the egg in the Characeæ,[21] which leads him to consider the group as independent of the algæ and derived from the primitive type of the archegoniates, just as the mosses and ferns. The *Wendungszellen* of Nitella he regards as a reduced archegonium wall, and the peculiar separation of a portion of the nuclear substance reminds one of the formation of a ventral canal cell.—C. R. B.

DR. F. NOLL proposes[22] the use of the scape of dandelion for demonstrating the mechanics of tendril coiling. By cutting out from the scape a long strip not much wider than thick, and, after fastening the two ends so that they cannot rotate, immersing the preparation in water, the inner tissues elongate so greatly that the strip is thrown into a spiral coil with one or more points of reversal, thus imitating very closely a huge tendril.—C. R. B.

ACCORDING to Palladine,[23] though light is not requisite for the regeneration of proteids, if cane sugar is supplied to the etiolated leaves of *Vicia Faba* under experimental conditions, the regeneration goes on more energetically in light than in darkness, and for this the more refrangible light is the more efficient. Such leaves cultivated on cane sugar solution in light respire more than twice as actively as when kept in darkness.—C. R. B.

DR. OSCAR LOEW brings together a useful summary of the present knowledge of the physiological rôle of mineral salts.[24] Unfortunately the greater part of the earlier experimentation in this direction has been more or less misguided, and one must hold very loosely the conclusions reached. This summary, however, will be useful as a guide to the literature of the subject.—C. R. B.

[20] Bot. Cent. **82**: 161–168, 194–200. 1900.

[21] Inaug. Diss. Freiburg. 1899. See Bot. Cent. **81**: 366. 1900.

[22] Flora **86**: 388. 1899. [23] Revue gén. de Bot. **11**: 81–105. 1899.

[24] LOEW, O.: "The physiological rôle of mineral nutrients." Bull. 18, U. S. Dept. Agric., Division of Veg. Physiol. and Path. 8vo, pp. 60. Washington: Gov. Printing Office, 1899.

OF GREAT INTEREST to all botanists is the report of Henry Gannett[25] on the forests of the United States. The author as chief of the Division of Geography and Forestry of the U. S. Geological Survey has had long and intimate acquaintance with the subject. It seems that on July 1, 1899, there were thirty-seven government forest reserves, aggregating 72,139 square miles, composed mainly of mountainous, rugged country, of no value for agriculture, but especially favorable for tree growth. The states containing these reserves are Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, South Dakota, Utah, Washington, and Wyoming. Of these Washington has much the largest proportion, 19 per cent. of the total area of the state being thus reserved. The bulk of the publication consists of abstracts of reports on forest reserves by special agents sent to examine them. — J. M. C.

TO THE LIST of seeds whose germination is affected by light, Heinricher adds our common *Veronica peregrina*.[26] Light, even weak light, accelerates germination, as a difference of five to eight days between light and dark cultures strikingly shows. The effect of the light depends apparently upon its action in promoting the digestion of the reserve foods.—C. R. B.

OSWALD RICHTER recommends[27] a concentrated solution of ammonia, used boiling, at 40° C., or cold, as a maceration fluid. He finds it much superior to the usual acids, because the cell wall is always intact. In many cases, also, the cell contents are preserved and even made clearer.—C. R. B.

PROFESSOR DR. S. ROSTOWZEW has devised,[28] apparently independently, the laboratory table with trapezoidal top, identical in form with that considerably used in this country when window space is scant. The form was first suggested, we believe, by Dr. C. E. Bessey.—C. R. B.

[25] Extract from Twentieth Ann. Rep. U. S. Geol. Surv., Part V, Forest Reserves. Pp. 1–37, with 7 maps. 1900.

[26] Ber. d. deutsch. bot. Gesells. **17**: 308. 1899.

[27] Oesterr. Bot. Zeitsch. **50**: 5–11. 1900.

[28] Bot. Cent. **81**: 361. 1909.

NEWS.

DR. E. B. COPELAND, assistant professor of botany in the University of West Virginia, has been advanced to a professorship.

DR. HUGO ZUKAL, professor of plant pathology in the Hochschule für Bodencultur in Vienna, died on February 15. (Bot. Cent.)

THE OFFICERS of the Botanical Society of America for 1900–1 are as follows: *President*, B. D. Halsted; *Vice President*, R. A. Harper; *Treasurer*, C. A. Hollick; *Secretary*, G. F. Atkinson; *Councillors*, B. D. Halsted, R. A. Harper, C. A. Hollick, G. F. Atkinson, B. L. Robinson, C. E. Bessey, and F. V. Coville; *Custodian of Library*, W. Trelease.

THE DIVISION of Vegetable Physiology and Pathology has just completed an extensive series of experiments at Halstead, Kan., in connection with work on the development of new forms of cereals by breeding. The work was planned by Mr. M. A. Carleton, but owing to his absence abroad it was carried on by Mr. D. B. Swingle, a graduate of the Agricultural College at Manhattan, Kan.

WM. J. FOX, of the Philadelphia Academy of Sciences, has had the good fortune to discover in the library of the academy a copy of that very rare work of Rafinesque entitled *Western Minerva*, or *American Annals of Knowledge and Literature*. Rafinesque proposed to publish a journal with this title, but only a single number appeared, bearing the date 1821, and, being suppressed by the printer, Rafinesque states that he only saved three copies of it. Mr. Fox gives a very complete account of the contents of the work in *Science* of August 10, 1900. It is a small quarto and contains vi + 82 pages, and is of interest to botanists in that it contains new names for plants which have not yet been noted in synonymy. It is an interesting question whether a work suppressed by the printer, and presumably never distributed, can be counted as a publication. In the copy discovered by Mr. Fox some of the pages are orginal proof sheets, being printed on one side only, containing corrections, and also such notes as "I must see another proof." It would seem necessary to distinguish between publication and printing, and the *prima facie* evidence is that this discovered pamphlet, although of great interest, does not come within the definition of a publication when the question of priority is concerned. Only four pages are given to botany, and Mr. Fox gives very fully their contents.